ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

ERRATA

Page 167, 5th line from bottom of page—Should read: Colorado: Baca, Denver, Fremont, and Weld counties.

Page 167, following line beginning New Mexico—Insert Oklahoma: Texas County.

September cover, line 9 of Contents—*Salva* should read *Salvia.*

Page 316, last line—St. James County should read Phelps County.

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A Quarterly Journal containing Scientific Contributions from the Missouri Botanical Garden and the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

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FEBRUARY, 1954

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Vol. 41 FEBRUARY, 1954 No. 1

THE NORTH AMERICAN SPECIES OF ASCLEPIAS L.*

ROBERT E. WOODSON, JR.

WITH DRAWINGS BY ELSIE H. FROESCHNER AND ALBERT A. HEINZE

INTRODUCTION

It has been over fifteen years since I began studies toward this revision. The long delay certainly has not been due to difficulty in specific delimitations, as is so frequently the case in genera of similar size; the species, for the United States at any rate, are unusually well defined and properly appreciated by the botanical public. Although this scarcely has been as true for the species of Mexico and Central America, I have occasionally wondered, through the years, whether it were not a waste of time to expend so much effort in attempting to distinguish species which already are such common knowledge.

But my primary purpose, when I began the study of Asclepiadaceae, was a definition of generic rather than of specific levels. The species of the family, as I have intimated, are for the most part very sharply defined; too sharply, one might almost say, since their differences so frequently are of the magnitude for genera in other families of Flowering Plants. This effect perhaps is a result, at least in part, of the extreme entomophily of asclepiads, as one might be led to believe by Stebbins' amplification of Schmalhausen's principle.

The vexing problems of generic limits amongst the Asclepiadaceae of North America were joined in the first paper[1] in this series. A greatly simplified system, having much in common with Decaisne's[2] for De Candolle's 'Prodromus', was the outcome. I still believe it to be the sensible course, conducive both to ready identification and to a proper perspective of evolution within the family. The reader, provided with Mrs. Froeschner's and Mr. Heinze's excellent drawings, may judge for himself.

When I began this series it was my intention, after reforming the generic limits for North America, to pass to the species of each genus in turn. This may not

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[1] Woodson, R. E., Jr. The North American Asclepiadaceae I. Perspective of the genera. Ann. Missouri Bot. Gard. 28:193. 1941.

[2] Decaisne, J. Asclepiadaceae, in DC. Prodr. 8:490. 1844.

*With the support of a grant from the American Philosophical Society.

now be realized except for *Asclepias,* which was the first on the agenda. And although *Asclepias* is not the genus most in need of revision, it will provide an illustration of what I consider to be the virtues of a conservative view of genera within the family as well as a fascinating example of the evolutionary consequences of entomophily.

The long delay, aside from the routine duties which nearly every one has to face, has been due rather to the irresistible array of fascinating and complex biological questions with which asclepiads divert attention. What of the origin and function of the marvelous apparatus for pollination by insects, and of its evolutionary significance? What of the intriguing population dynamics suggested by our rich herbarium collections? It has been relatively an easy matter to check the varying accounts of the pollinating apparatus and to add what little I could. Such aspects of asclepiads have attracted the attention of botanists for nearly two centuries. Other diversions have been more consequential.

Relatively early in these studies—ten years ago or so—I became diverted by the absorbing population patterns of a single species: *Asclepias tuberosa.*[3] Involving nearly half the area of the United States, together with contiguous portions of Canada and Mexico, this problem has claimed most of my meagre research time ever since, and more remains to be done. Other similar patterns, but with their unique variations, certainly exist in other species, such as *A. incarnata* and *A. asperula.* Even more fascinating may be the apparent *artenkreiss* involving *A. incarnata, A. fascicularis, A. subverticillata,* and *A. verticillata,* and the neutral polymorphism of *A. viridiflora;* the peculiar complementary clines apparent in the fruit of *A. syriaca* and *A. speciosa* doubtless will repay attention. And there are others. I look forward to them as far as time permits.

Meanwhile, however, the general *mise en scène,* in the form of this revision, should be delayed no longer or it may be never. That it is completed at last I owe to the American Philosophical Society, which enabled me to unload much onerous detail upon the capable shoulders of my student and friend Ding Hou.

COMPARATIVE MORPHOLOGY

HABIT:—

The twining habit so characteristic of the Asclepiadaceae is wholly absent from *Asclepias.* The North American species are erect herbaceous perennials predominantly; but the ubiquitous tropical and subtropical *A. curassavica* (which I believe actually may be indigenous to South America) is an annual, as are also the Antillean *A. nivea* and the Mexican *A. angustifolia.* A few species, particularly of the Gulf of California region, such as *A. albicans* and *A. subulata,* develop into twiggy shrubs.

With the exception of very few species (viz. *A. tuberosa* and *A. longifolia*) all organs of *Asclepias* are traversed by an intricate system of latex canals which are

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[3] Woodson, R. E., Jr. Some dynamics of leaf variation in *Asclepias tuberosa.* Ann. Missouri Bot. Gard. 34:353. 1947.

responsible for names "milkweed," commonly applied to the genus in the United States and Canada, and *lechetresna* in Mexico and Central America. Neither the latex nor the prominent pericycle and phloem fibers, also frequent amongst the species, has been exploited commercially. The stele is bicollateral, as in most Contortae.

I know of no truly rhizomatous North American species, but some, as *A. syriaca,* may produce gemmiferous roots giving rise to clons of limited extent. In numerous species the perennial caudex (derived from the hypocotyl) becomes quite stout and produces annually a crop of several herbaceous flowering stems, numbering more than 50 per plant in *A. tuberosa* occasionally. In several the caudex becomes a conspicuous napiform body. Plants of *A. tuberosa* certainly attain a very great age for herbaceous perennials, and the shrubby thickets of *A. subulata* must frequently be over a century old. Even the annual *A. curassavica* may live for several years by proliferating new flowering branches from the cauline nodes.

LEAVES:—

The leaves usually are decussate. In several species, notably *A. tuberosa, A. viridis,* and *A. asperula,* they are rather irregularly spiral, while those of *A. verticillata* and its relatives are more or less irregularly whorled. *Asclepias quadrifolia* is of particular interest in that, although the leaves are decussate, one internode at the middle of the stem customarily is condensed to form a false whorl of four leaves; this process repeated is apparently the origin of the verticillate foliage of other species. In all species which I have cultivated, seedling leaves are decussate and this, it must be held, is the primitive phyllotaxy.

Since leaves of all Asclepiadaceae are simple and entire, in so far is the leaf outline of the North American species restricted. In all other respects, however, variation is wide. Many species produce the glandular emergences upon the upper surface frequent for the entire family but these, unlike the situation in Apocynaceae, can seldom, if ever, be used diagnostically. An interesting adaptation to aridity is found in several of the shrubby species of the Gulf of California region, such as *A. subulata, A. leptopus,* and *A. albicans* and its close relatives. In these the sparse linear leaves of the young stems become caducous upon development of inflorescences; one seldom finds leaves upon herbarium specimens as a consequence. Photosynthesis here is conducted principally by the green twiggy stems which may be covered with waxy cutin to restrict transpiration.

INFLORESCENCE:—

The inflorescence of *Asclepias* is representative of the tribe Asclepiadeae as a whole. It is an umbelliform cyme, either terminal or lateral and interpetiolar. A striking feature of the umbelliform cyme is for the flowers to mature not in a strictly determinate succession but rather in an irregularly centripetal fashion. This is explained by occasional abnormal inflorescences which develop a more elongate, obviously geniculate rachis, demonstrating the "umbel" to have been derived through condensation of a cincinnus. It also establishes the nearly hemispheric or spheric shape.

The interpetiolar position of the inflorescence is an anomaly which has intrigued morphologists for over a century. Most have concluded that such inflorescences, although lateral superficially, actually are terminal historically and that the axis system, although monopodial superficially, actually is a sympodium. With this view my own observations agree. A summary of the shoot system of *Asclepias curassavica* will illustrate the basic conditions for the genus as a whole.

Although not apparent to a casual observer, the leafy axis of *A. curassavica* consists of two well-defined regions: a basal and vegetative, and an upper and flowering. Both are erect and confluent and both bear decussate leaves. In the basal vegetative region adjacent pairs of leaves are perpendicular to one another and each leaf of a pair subtends a bud, one weakly and the other more strongly developed. The strong and the weak buds, collectively, describe parallel spirals through successive nodes. In most species of *Asclepias* neither bud develops further, and frequently even the strong bud is quite difficult to see except in dissection. In *A. curassavica,* one or more of the strong buds may eventually develop into a leafy and flowering secondary axis following the flowering or decapitation of the primary. In *A. incarnata,* on the other hand, the strong buds regularly develop into stout flowering branches. The weak buds seem either to be quite incapable of further growth or capable of producing only very stunted development under such abnormal conditions as extreme decapitation or senescence.

Upon the attainment of flowering age, the shoot of *A. curassavica* becomes changed in three respects. Firstly, pairs of leaves, formerly perpendicular to adjacent pairs, become oblique, two such pairs intersecting through two obtuse angles of approximately 120° and two acute of approximately 60°. Secondly, the strong and weak buds, instead of describing the parallel spirals noted in the vegetative portion of the stem, assume rectilinear sequences confined to two adjacent vertical orthostichies respectively to either side of the obtuse angles formed by the adjacent pairs of leaves. Lastly, the flowering peduncles appear, one to each node and inserted slightly to the right and left, successively, of the leaves subtending the strong buds, as in fig. 1. When viewed facing the obtuse angles formed by the leaves, the young flowering stem appears nearly rectilinear or very slightly skewed to the right or left at the tip; when viewed facing the acute angles, the stem has the zigzag configuration of a rhipidium. These aspects are lost upon the advent of secondary growth of the stele.

But slight variations from this plan appear throughout the genus, except in *A. tuberosa,* which will be described presently. Although it is usual for the peduncles to be inserted slightly to the right or left of the leaves subtending strong buds, the insertion is exactly interpetiolar in numerous species, as in *A. angustifolia.* Again, numerous species produce solitary terminal inflorescences; in these the uppermost pair of leaves is more or less oblique, which renders the interpretation

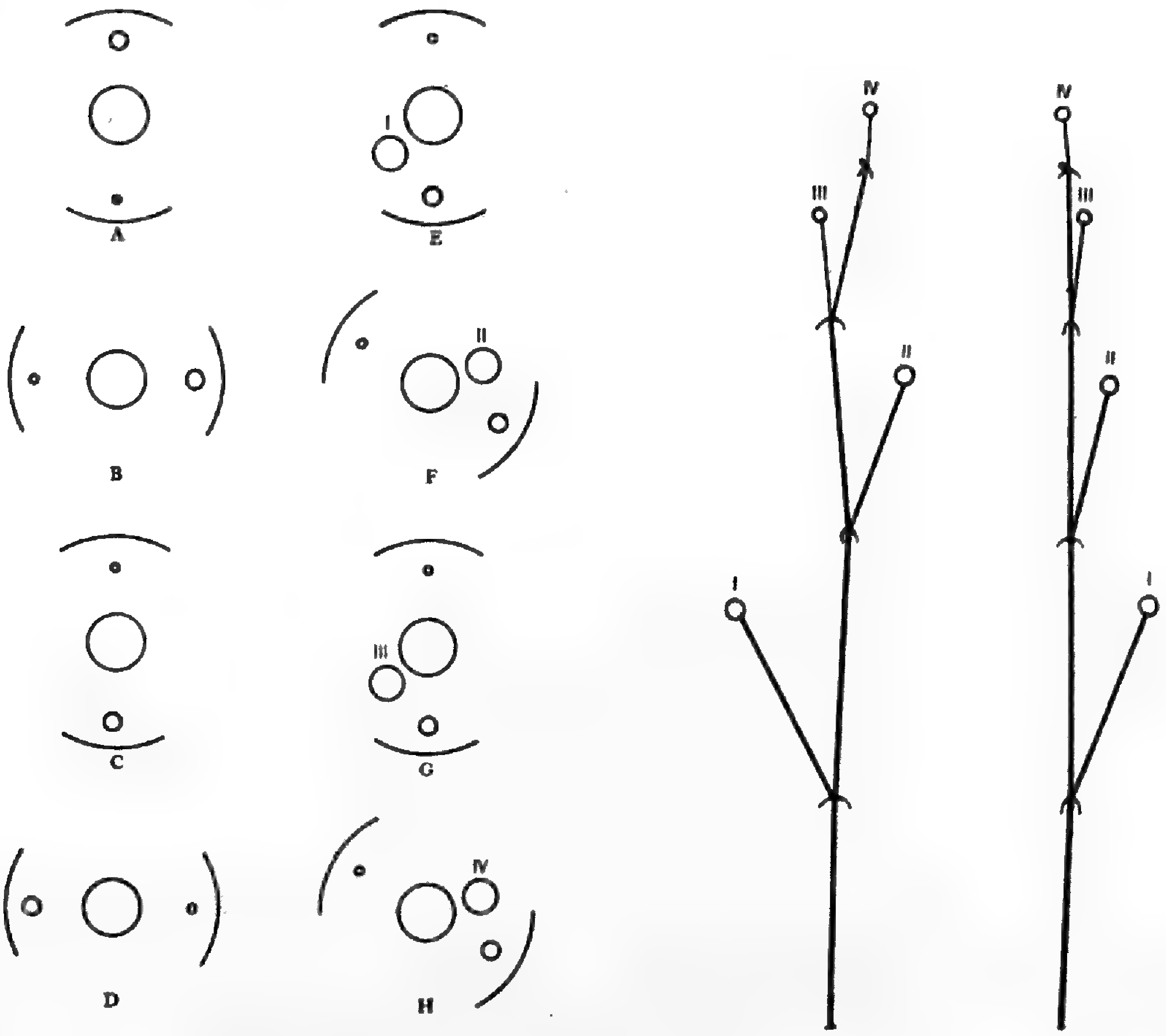

Fig. 1. *Asclepias curassavica.* A–D: vegetative nodes; E–H: flowering nodes. Explanation in the text.

of the solitary peduncle as historically the lowermost of such an interpetiolar series as that observed in *A. curassavica.*

In such species with whorled leaves, as *A. fascicularis* and *A. mexicana,* there is a tendency for the number of peduncles at a given node to correspond to the number of leaves; in *A. verticillata,* although the number of leaves in a whorl tends to be four or five, the peduncles usually are solitary. In *A. incarnata,* the upper nodes usually bear paired peduncles—one to either side of the "fertile" leaf, but this occasionally is accompanied by such more obvious signs of fasciation as irregularly whorled leaves and a flattened subtending internode.

Asclepias tuberosa differs from all other species of the genus in that the upper flowering region of the leafy axis is quite conspicuously distinct from the lower vegetative region. The latter is more or less decumbent to essentially erect, normally does not branch vegetatively, and bears numerous irregularly scattered leaves with a vague tendency to group in opposite pairs. The flowering region consists usually of two to several more or less elongate and deliquescent branches of an unmistakably scorpioid appearance. The leaves, progressively reduced in size, usually are definitely organized into decussate pairs obliquely intersecting with obtuse and acute angles of approximately 140° and 40° respectively; the obtuse angles are dorsiventral to the deliquescent axis, which contributes further to its scorpioid appearance.

The axis is rendered scorpioid by its composition into progressively shortened sympodial constituents, each terminated by an ascending flowering peduncle almost exactly interpetiolar to the pairs of leaves in the upper obtuse angles, as illustrated in fig. 2. The scorpioid aspect here is observed when the flowering branch is viewed in profile, viz. facing the acute angles of the leaf pairs. When viewed from above, viz. facing the upper obtuse leaf angles, the axis appears somewhat zig-zag due to the association of the flowering peduncles with the slightly decussate leaves.

The flowering axis of *A. tuberosa* is so obviously and incontrovertibly sympodial and scorpioid that it is unfortunate that few morphologists who have studied the shoot of *Asclepias* apparently had access to it. The difference in aspect between the flowering axes of *A. tuberosa* and *A. curassavica* is wholly due to the fact that the former is deliquescent and the latter erect. The erect position obviously is derived from the deliquescent as seen in the persistent obliquity of the decussate pairs of flowering leaves, in *A. tuberosa* the effect of the dorsiventrality of the deliquescent axis.

A comparison of fig. 2 for *A. tuberosa* with fig. 1 for *A. curassavica* demonstrates that in both the flowering axis is scorpioid, the sympodium appearing alternately to the right or the left of the "fertile" leaf associated with the flowering peduncles. The difference is solely the alternate shift of the peduncles to the right or left of the "fertile" leaf which occurs in *A. curassavica.* This must be due to the change in polarity of the flowering shoot as a whole, *i.e.* from the deliquescent to the erect position.

Although the strong and weak axillary buds are observed in *A. tuberosa* only upon dissection, it is found that in this species, as in *A. curassavica,* they occur in pairs of opposed orthostichies separated by the two obtuse angles formed by the oblique intersection of the adjacent pairs of leaves. In both species the functional axis of the sympodium is associated with the "sterile" leaves, *i.e.* those subtending the weak buds.

Since a monochasium in plants bearing decussate foliage is ordinarily derived through modification of a dichasium, we may next search for the missing complementary sympodium. This surely must be represented by the strong axillary buds which, in fact, occasionally develop short flowering branches in *A. tuberosa.*

There remains to explain the weak buds of the orthostichies of leaves which, according to my view, historically subtend the axes composing the sympodium. Certain formalistic morphologists, in my position, probably would dismiss the weak buds as "accessory" or "supernumerary." This I also am prepared to do. It is an anatomical axiom, probably as well as a physiological necessity, that an angiospermous leaf should subtend a bud; whence the appearance of an accessory bud after the assumption of the functions of a primary axis by the erstwhile axillary branch.

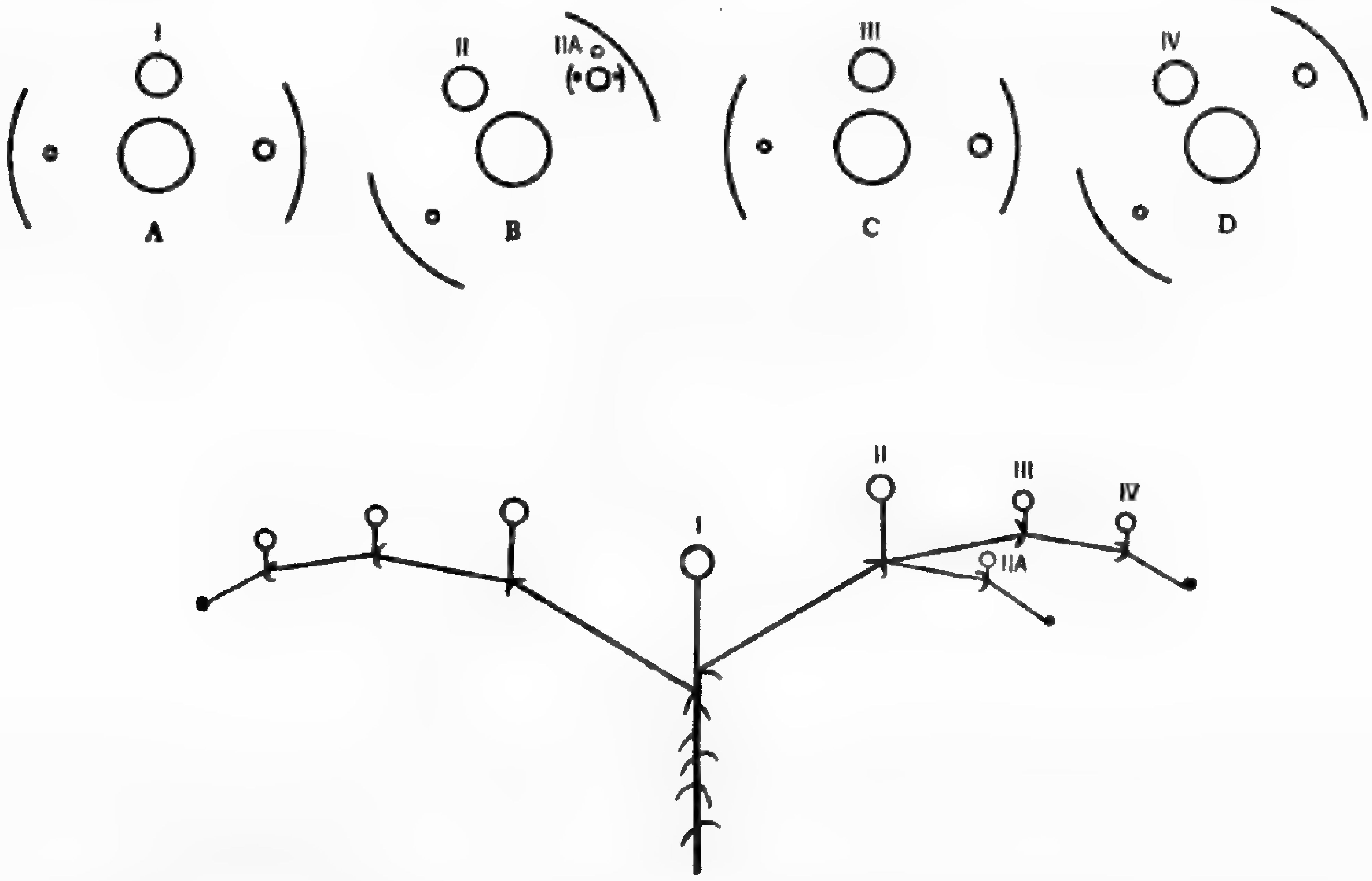

Fig. 2. *Asclepias tuberosa.* A–D: flowering nodes. Explanation in the text.

It follows that the vegetative basal portion of the leafy axis of *A. curassavica,* and probably all other species of the genus, is helicoid and a bostryx, while the upper flowering portion is scorpioid and a cincinnus.

Much effort has been expended by morphologists, from the time of the Bravais brothers[4] in 1837 to that of Schoute[5] a century later, in attempting to explain why the terminal peduncles of asclepiads should be interpetiolar and not placed in the axil of the leaves. The Bravais' conceived the notion that the cause was crowding out *(déjetement)* of the peduncle by the strong bud, and in this they are followed by Schoute who, however, finds it a bit difficult to explain why the "*déjetement*" should be complete in some cases and only partial in others. Just why a terminal axis should be required in an axillary position appears difficult to reconcile. While recognizing that morphologically terminal flowers in uniparous cymes frequently do appear to be subtended by a leaf or bract, their association with it should be understood as a derived one and in no sense historical. It appears to me wholly gratuitous to argue that the admittedly terminal peduncle has been crowded from an axillary position by the notably quiescent "strong" bud, with which the peduncle is associated only because the "strong" bud is the missing sympodium of the former dichasium. If both were axillary and actual pressure a factor, one would expect the bud to be displaced instead.

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[4] Bravais, L., and A. Bravais. Essai sur la disposition symétrique des inflorescences. Ann. Sci. Nat. Ser. II, 8:11. 1837.

[5] Schoute, J. C. The interpetiolar inflorescence of *Vincetoxicum* and *Asclepias.* Rec. Trav. Bot. Néerl. 34:182. 1937.

An interesting historical summary of various rationalizations of the interpetiolar inflorescence has been compiled by Schoute,[6] to which the reader is referred. Schoute founds his own contribution, which deals with but one species of *Asclepias* (*A. curassavica*), upon the assumption of a primitive spiral phyllotaxy. According to him, the alternate weak and strong buds are proof that the leaves have been laid down in a spiral from which, by metopy, a decussate readjustment has been made. This is maintained in spite of the fact, which we already have noted, that the juvenile phyllotaxy of all asclepiads is decussate, whatever the arrangement in the adult, and that by far the predominant adult phyllotaxy not only of Asclepiadaceae but of such related families as Apocynaceae, Gentianaceae, Loganiaceae, and Oleaceae, is decussate as well.

Having elected the spiral as the primitive phyllotaxy, Schoute considers the question whether the strong buds are in the axils of the upper or the lower leaves in the broken spirals composing the decussate leaf pairs. By a series of formalistic diagrams and the assumption that the peduncles were originally axillary, he comes to the conclusion that the strong buds are subtended by the upper leaves and the weak buds (taken as of equal structural value to the stronger) subtended by the lower. No explanation of the inequality is advanced, contrary as it is to ontogenetic expectation.

As a further consequence of the hypothesis of spiral phyllotaxy, we are forced to the corollary of a primitive condition of alternate fertile and sterile nodes, a formidable anomaly in itself. Incidentally, for *A. curassavica* Schoute[7] figures a spiral of three bracts borne upon the flowering peduncle. These, in fact, are quite fictitious, since the peduncles of all species of *Asclepias* are naked. As an important confirmation of his theory of basic spiral phyllotaxy, Schoute also figures alternate interpetiolar hair-lines for the leaf pairs of *A. curassavica.* Although I have seen such alternate hair-lines in *A. incarnata* and other species, my own cultures of *A. curassavica,* grown from seed, invariably show opposite hair-lines. Variability in this respect may well involve a relatively simple Mendelian solution. It is also rather disturbing for Schoute to quote the Bravais', quite without dispute, that in *A. syriaca* the peduncles are "placed almost exactly between the two petioles, whereas in *A. tuberosa* [there is] very little extra-axillarity,"[8] when the true situation is exactly the reverse.

FLOWER: CALYX:—

The flowers of *Asclepias* invariably are actinomorphic. The calyx consists of five equal and essentially separate, ovate to lanceolate, more or less foliaceous lobes which are open in aestivation. At their base, within, usually may be found few to several minute glandular emergences ("squamellae") which are the homologues of the foliar and nodal glands as in Apocynaceae.[9] They appear to have no diagnostic value in *Asclepias.*

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[6] Schoute, J. C. loc. cit. 1937.
[7] Schoute, J. C. loc. cit. *fig. 2.* 1937.
[8] Schoute, J. C. loc. cit. p. 191. 1937.

COROLLA:—

The corolla is rotate, with an extremely shallow annular tube. The five equal lobes, valvate or barely contorted in aestivation and usually ovate-elliptic in outline, ordinarily are sharply reflexed at anthesis but in numerous species spread horizontally. In *A. pedicellata* the narrow corolla lobes are erect or nearly so, imparting a tubular aspect. Coloration is in various shades and combinations of white, red, or yellow, occasionally with a suffusion of purple.

GYNOSTEGIUM: ANDROECIUM:—

The fascination of the asclepiad flower resides in the stamens. Five in number and antesepalous, the stamens are united with the fleshy *stigma head* to form the characteristic structure of Asclepiadaceae known as the *gynostegium*. The filaments are coherent into a tube known as the *column* and adnate collectively to the base of the annular corolla tube.

The bilocular anthers are rather broadly oblong or subquadrate and tipped with a triangular hyaline appendage inflexed over the stigma head. The outer lateral margins of each are bordered with more or less dilated, frequently corneous *wings* which are applied nearly face to face with the adjacent wings of the neighboring anthers and at an obtuse angle to the back of each. The anther wings guard the entrances to the five *stigmatic* (or "alar") *chambers* and frequently are notched or spurred, an ornamentation which may be connected in some way with selective pollination. The anthers are somewhat flattened dorsiventrally; the two vertical pollen sacs dehisce introrsely by a prominent apical pore.

Although the anthers appear dorsally to be free from one another because of their prominent wings, actually they are completely coherent ventrally except near their tips; conversely, the coherent portions of the anthers are free from the stigma head (although closely applied to it) except near their tips where the wings are strongly adnate separately, and at the base where they form an adnate ring. It thus obtains that the so-called "stigmatic chambers" actually are formed by the anthers themselves, except at their tips where access is gained to the true stigma (pl. 3, fig. 1).

CORONA:—

The most variable structure of asclepiadaceous flowers is the *corona* which, in *Asclepias*, consists of five separate organs, the *hoods*, borne at the summit of the column and subtending the anthers. Alternating with the hoods are five minute, more or less ligular organs, sometimes entire but usually more or less deeply bifid and involute under the paired anther wings, which I call the *alternating lobules*. The hoods obviously are enations of the staminal filaments and have their simpler counterparts in several other families of Angiosperms (cf. *Forsteronia* subgen. PTERANTHERA of Apocynaceae). The alternating lobules, on the other hand, probably are of double nature and constituted in part by each of the adjacent stamens; but this is more easily demonstrated when they are deeply bifid and less

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[9] Woodson, R. E., Jr., and J. A. Moore. The vascular anatomy and comparative morphology of apocynaceous flowers. Bull. Torrey Bot. Club 65:135. 1938.

so when entire. The hoods are nectaries and provide the attraction for the insect visitors. One frequently finds them overflowing with viscid colorless nectar shortly after anthesis of the flower. Upon several occasions I have found a hood to contain a single colorless transparent crystal of tabular form and measuring more than 1 mm. square, obviously condensed from the nectar.

The hood has been the chief source of the generic segregates of *Asclepias*. It is a rather complex organ and its variations almost defy description. In what I take to be its primitive form, the hood is a simple shovel- or scoop-shaped body of delicate texture, open at top and front, attached to the column by a short but slender substipitate base, and bearing within toward the base a slender incurved acicular process of slightly greater length which is called the *horn*. The papillate cells which secrete the nectar are found chiefly toward the base of the horn.

PHYLOGENY OF THE HOOD:—

Diversification of the hoods seems to have proceeded in the following directions although not always *seriatim:* 1, generally toward a more fleshy texture; 2, toward elimination of the substipitate base through decurrence upon the column until a deep pouch is attained; 3, elongation and deflection and involution of the margins to produce a clavate form; 4, elimination of the horn through various degrees of adnation; 5, basal prolongation upward to produce a more or less elevated *stipe* bearing the alternating lobules and the anther head at the summit. In varying degrees more or less consistent with these trends of the hoods both the column and the anther head become broader and more squat until, in the final series and subgenera, the column is virtually eliminated and the gynostegium is essentially sessile.

By far the greatest number of the North American species of *Asclepias* are included within the "primitive" subgenus ASCLEPIAS. Here systematization of the species upon a continental scale is really a difficult matter and upon it I have spent most of the years of this study, particularly upon fresh flowers which I have obtained in the field, and flowers in "spirits" sent me by a host of generous friends and acquaintances. The result, I fear, is what will appear to be a decidedly recondite system based upon the natural contours of the hoods particularly with respect to the dorsal view: whether broadly rounded, broadly flattened (compressed tangentially), or more or less sharply keeled (compressed radially).

These details have been generally ignored previously, as the shapeless, baggy hoods of even the best of previous illustrations usually will witness. Unfortunately, they are difficult to observe from herbarium specimens at times. But they are consonant with the more general phylogenetic diversifications which have been discussed above: both the rounded and the flattened types appear to be primitive as seen by their nearly free horns and tendency toward substipitate bases; the keeled type would be advanced because of its usually strongly adnate horn and tendency toward a basal pouch. Such are the phylogenetic sequences upon which I have constructed my classification of the North American species. They are beautifully illustrated by Mrs. Froeschner and Mr. Heinze in the taxonomic section which follows.

GYNOECIUM:—

The gynoecium of *Asclepias* is quite typical of the family. It consists of two wholly superior carpels completely free save at the common ***stigma head.*** The ovules are anatropous and multiseriate upon the ventral placenta. The stigma head is a relatively massive structure supported by the free styles of the carpels from which it is rather abruptly produced; it is roughly an inverted and truncate, pentagonal pyramid, the sides of the pentagon formed by the connivence of the five anthers.

Although the top of the stigma head has an epidermis of papillate cells they are not glandular and do not receive the pollinia, as is well known. The lateral "angles" of the pentagon are scarcely such, geometrically speaking, for they are truncate and furrowed, and it is here that the secretory epidermis is located (pl. 2, fig. 1). These five furrowed "angles" of the stigma head are roughly in the form of a cross with obliquely descending arms. The head and the arms of the cross, of varying dimension and contour characteristic of each species, are the place of origin of the translator apparatus of the pollinia; the foot of the cross is the receptive surface of the stigma.

POLLINIUM:—

In 1811 Robert Brown[10] separated his natural order Asclepiadeae from the Apocineae of Jussieu upon the basis of the highly specialized pollinia of the former. His differentiation of the two groups remains the boundaries of the present-day families Asclepiadaceae and Apocynaceae, respectively.

Although quite analogous to those of the orchids the ***pollinia*** of asclepiads are a much more elegantly contrived apparatus for entomophily. Two special forms exist in the family characteristic of the subfamilies Periplocoideae and Cynanchoideae. Those of the latter, which includes the genus *Asclepias,* consist of two (or four in the tribe Secamoneae) completely enclosed packages of pollen grains (***pollinium sacs*** or pollinia proper) united by more or less of a yoke-like process of each (***translator arms*** or retinacula) to a common sagittate body known variously as the ***gland*** or corpusculum.

The gland, as we shall refer to it here, is dark brown usually and of a corneous consistency; it is compressed radially, with the inner surface smooth and entire but the outer with a narrow slit passing almost completely through it from top to bottom. This slit is of the utmost importance to its transportation by insects.

The translator arms, sometimes virtually lacking in genera other than *Asclepias,* are usually more narrow, often quite elaborately winged or fluted ribbons of yellow cartilaginous substance attached at either side toward the base of the gland, on the one hand, and on the other, to the tips of the pollinium sacs. The pollinium sacs, of semi-transparent yellowish substance, in *Asclepias* are strongly compressed, more or less asymmetrically pyriform bodies pendulous from their respective translator

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[10] Brown, R. On the Asclepiadeae. Mem. Wern. Soc. 1:12. 1811.

arms. Under magnification the pollinium sacs appear as a faint mosaic of roughly hexagonal areolae which mark the position of the pollen grains.

Although the essential function of the pollinia of asclepiads had been recognized at least as early as Tournefort, their exact nature and origin were in doubt not only in the time of Robert Brown but for over a half century subsequently. That doubt should continue after Brown is scarcely conceivable; for with his characteristic inquisitiveness and insight (as well as his habitually laconic simplicity) he had discovered the basic facts of the development of the pollinia of *Asclepias syriaca* from fresh dissections alone and with only the crude magnifiers of his age. Scarcely a better introduction to the development of asclepiad pollinia, nor tribute to the acuity of Brown, could be provided than his own words:[11]

> "The flower-bud of this plant [*Asclepias syriaca*] I first examined, while the unexpanded corolla was yet green and considerably shorter than the calyx. At this period, the gland-like bodies which afterwards occupy the angles of the stigma were absolutely invisible; the furrows of its angles were extremely slight, and, like the body of the stigma, green; the antherae, however, were distinctly formed, easily separable from the stigma, and their cells, which were absolutely shut, were filled with a turbid fluid, the parts of which did not so cohere as to separate in a mass; of the cuculli [hoods], which in the expanded flower are so remarkable, and constitute the essential character of the genus, there was no appearance.
>
> "In the next stage submitted to examination, where the corolla nearly equalled the calyx in length, the gland-like bodies of the stigma were become visible, and consisted of two nearly filiform, light brown, parallel, contiguous and membranaceous substances secreted by the sides of the furrow, which was now somewhat deeper: Instead of the filiform processes [translator arms], a gelatinous matter occupied an obliquely descending depression proceeding from towards the base of each side of the angular furrow.
>
> "In a somewhat more advanced stage, the membranes which afterwards become the glands of the stigma, were found to be linear, closely approximated, and to adhere at their upper extremity. At the same time, the gelatinous substance in the oblique depression, had acquired a nearly membranaceous texture and a light brown colour, and on separating the gland from its furrow, which was then practicable, this membrane followed it. At this period, too, the contents of each cell of the anthera had acquired a certain degree of solidity, a determinate form, and were separable from the cell in one mass; the cuculli were also observable, but still very small and green, nearly scutelliform, having a central papilla, the rudiment of the future horn-like process. Immediately previous to the bursting of the cells of the antherae, which takes place a little before the expansion of the corolla, the cuculli are completely formed, and between each, a pair of minute, light green fleshy teeth [alternating lobules] are observable, the single teeth of each pair being divided from each other by the descending alae of the antherae. The glands of the stigma have acquired a form between elliptical and rhomboidal, a cartilaginous texture, and a brownish-black colour; they are easily separable from the secreting furrow, and on their under surface there is no appearance of a suture, or any indication of their having originally consisted of two distinct parts; along with them separate also the descending processes, which are compressed, membranous, and light brown; their extremity, which is still unconnected, being more gelatinous but not perceptibly thickened. The pollen has acquired the yellow colour and the degree of consistence which it afterwards retains. On the bursting of the cells, the gelatinous extremity of each descending process becomes firmly united with the upper attenuated end of the corresponding mass of pollen . . ."

Contrary to what one might expect, the discerning observations of Brown were neither immediately accepted nor even subjected to verification. As late as 1857 the pioneer morphologist Payer[12] believed the "gland" of the pollinia to be a real

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[11] Brown, R. loc. cit. pp. 14–16. 1811.

[12] Payer, J. B. Traité d'organogénie comparée de la fleur. 1:569. Paris, 1857.

gland whose secretions trickle down the two descending furrows of each angle of the stigma head to form the translator arms, and finally into the anther loculi to cement the pollen grains. He had not observed, as had Brown, that the translator apparatus and the pollinium sacs must necessarily be formed independently since both are completed prior to dehiscence of the anthers!

ONTOGENY OF THE TRANSLATOR:—

It is a simple matter to verify and to amplify Brown's account of the origin of the translator apparatus with modern microtome sections. In very young buds of *Asclepias curassavica* the furrows of the five angles of the stigma are found to be lined with closely packed, deep, but exceedingly narrow secretory cells. The appearance of the gland is first noticed as two isolated lines of lipoid substance formed on the outer margins of the furrow (pl. 2, fig. 2). These thicken greatly, and their semi-solid nature is demonstrated by striations formed by the accretions from each glandular cell. In time, intervening cells of the furrow also become secretory, bringing together the originally isolated margins which have now become particularly thick and approximated, thus forming the dorsal slit (pl. 2, fig. 4).

The secretory cells of the obliquely descending furrows of the angles are not as closely packed, narrow, nor deep as those which secrete the gland. Their secretions are much more scanty and apparently more fluid since the translator arms which they form are not striated as is the gland. They stain very much less deeply with safranin than either the gland or the enclosing membranes of the pollinium sacs (pl. 2, figs. 5-6). A more detailed histological account of the development of the translators of *Asclepias syriaca* has been published by Corry[13], completely corroborating the account of Brown.

Robert Brown was unable to investigate the nature of the enclosing membranes of the pollinium sacs because of technical limitations of his age. Payer[14] also, limited to macroscopic dissections, could only conjecture concerning it. Both Brongniart[15] and Schleiden[16] considered the pollinium sacs to be confined by a cellular layer derived from outer sterile cells of the pollen mass, probably misled by the mosaic of hexagonal areolae previously noted above. Corry, much more convincingly, concluded that the vertical wall of each of the tapetal cells adjacent to the pollen grains undergoes "conversion into cutin", and that this change is followed successively by a like conversion of all the walls surrounding the pollen grains. This is not far from the truth.

A peculiar feature of microsporogenesis in *Asclepias,* as both Corry[17] and Frye[18] have ascertained, and as I also have observed in *A. curassavica, A. syriaca, A. verticillata,* and *A. viridis,* is for the archesporium to consist of numerous rather

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[13] Corry, T. H. On the mode of development of the pollinium in *Asclepias Cornuti* Decaisne [*A. syriaca* L.]. Trans. Linn. Soc. London 2:75. 1883.

[14] Payer, J. B. loc. cit. 1857.

[15] Brongniart, A. T. Quelques observations sur la manière dout s'opère la fécondation dans les Asclepiadées. Ann. Sci. Nat. Ser. I, 24:263. 1831.

[16] Schleiden, M. J. Principles of scientific botany, ed. 3., p. 356. 1849.

[17] Corry, T. H. loc. cit. 1883.

[18] Frye, T. C. Development of the pollen in some Asclepiadaceae. Bot. Gaz. 59:325. 1901.

elongate prismic pollen mother cells in a rather oblique, radial, and very compact tissue, each cell approximately as long as the radial dimension of the anther loculus (pl. 3, fig. 2). The cell walls separating the pollen mother cells are very thin, but never disengage from one another as is customary previous to reduction division in most other seed plants. Reduction division accomplishes the partition of the prismic pollen mother cell into a linear tetrad of pollen grains (pl. 3, figs. 3-4); neither do the walls of these disengage so that at maturity of the pollen the contents of the anther loculus still is a solid tissue. When mature the pollen contains the usual two nuclei (pl. 3, fig. 5).

I have been particularly interested in the tapetum, which is unusually massive. Although not mentioned by either Corry or Frye, but perhaps schematically figured by the former for *A. syriaca,* the tapetum of the four species which I have investigated is divided tangentially into two very different tissues dorsal and ventral to the loculus respectively (pl. 3, figs. 2, 6). The ventral or inner tissue, usually two or three cells deep, consists of cells rather typical for an angiospermous tapetum. The dorsal or outer tapetum, approximately six to twelve cells deep, consists of cells which are generally similar in outline to those of the ventral, and, like them, with one to three very prominent nuclei; but in addition they contain numerous lipoid bodies which stain very prominently with safranin. Similar but more minute bodies are found in the cells secreting the translator apparatus (pl. 2, fig. 3). It was doubtless the secretion of the tapetum which Robert Brown saw and described as a "turbid fluid" within the loculi of the young anthers of *Asclepias syriaca.*

The tapetum persists for some time after the formation of the linear tetrad of pollen grains which, as we have already remarked, are not separated but continue to lie in a solid tissue—also at this time in direct contact with the tapetum. The thin walls, apparently cellulosic, have stained with fast green in my sections. While the mass of pollen grains is still in contact with the tapetum, however, the outer containing walls of the pollinium sac (for of course such it is) suddenly show a slight affinity for safranin, and the stain becomes more and more pronounced, not only in the outermost walls but progressively noticeable also in the walls within (pl. 3, fig. 4).

About the same time, also, the loculus begins to expand and the tapetum to disorganize (the dorsal fatty tissue being last) until the pollinium sacs lie quite loose within the center of the loculus (pl. 3, fig. 5). By this time their outermost wall has become very intensely stained with the safranin and it is several times thicker than when the affinity for safranin was first noticed. The interior walls stain more deeply and have become somewhat more thickened also, but not to such a marked degree as the outermost wall. It is now that the anther dehisces by its apical pores and that the translator arms unite with the tips of the pollinium sacs (pl. 2, fig. 6).

Judging from the prominent lipoid bodies within the outer or dorsal tapetum, identical in their staining reaction to that of the pollinium sac membranes, I assume that it is the function of this tissue to secrete the required lipoid substance which the walls of the tetrads absorb, while the function of the ventral or inner tapetum would appear to be purely nutritive. In any event, it is obvious that the tapetum contributes only its secretions to the pollinium sac membranes which are, in fact, the walls of the coherent tetrads of pollen grains. Each pollen grain, therefore, is enclosed within its own polygonal compartment of thickened walls from which, incidentally, it lies quite free. In addition to these common walls the individual pollen grain possesses only a very thin intine (pl. 3, fig. 5). This has led some to describe the pollen of Asclepiadeae as possessing but a single spore coat, which is true functionally if not ontogenetically.

The membranes of the pollinia, secreted as they are in three sections and by two distinct organs, the stigma and the anther, appear of closely similar, if not identical, chemical constitution when subjected to routine microchemical tests. They apparently are of some form of suberin, staining deep orange when treated with 40 per cent potassium hydroxide. When the potassium hydroxide is heated to boiling, irregular aggregates of minute grains (potassium phellonate) appear; these become reddish violet when treated with a drop of chloro-zinc-iodide (equal parts of saturated zinc chloride and zinc iodide).

Repetition of these tests with microtome sections, cut at 10 μ in order to investigate the chemical reactions of the lipoid bodies of the tapetum, left much to be desired because of the macerating action of the potassium hydroxide and inability to clear the fragments of tissue. Definite orange discoloration of the tapetum was observed when treated with heated KOH. The suberin therefore appears to be secreted within the tapetum cells and later digested and translocated to the pollinium membranes.

POLLINATION:—

The entomophilous pollination of asclepiads provides one of the most fascinating chapters in biology, and one which many authors have loved to retell and to elaborate. Apparently Sprengel[19], in 1793, was the first to observe the extraction of pollinia by insects, although he was ignorant of the true location of the stigmatic surface and entertained several erroneous impressions such as ascribing a trigger mechanism to the gland. Robert Brown[20], in 1831, correctly located the stigmatic surface at the tips of the chambers formed by the contiguous anther wings and described the germinated pollinia which he found within them. In 1865 Delpino[21] published a detailed study to which little has been added since, although the subject has been treated variously by many subsequent authors including Charles Darwin.[22] The most comprehensive review is that published in 1883 by Corry[23]. Since I, myself, have nothing new to report, a very brief and generalized account will suffice here.

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[19] Sprengel, C. K. Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen. p. 139. Berlin, 1793.

[20] Brown, R. On the organs and mode of fecundation in Orchideae and Asclepiadeae. Trans. Linn. Soc. London 16:685. 1833.

[21] Delpino, F. Relazioné sull 'apparecchio della fecondazione nelle Asclepiadee. Torino, 1865.

[22] Darwin, C. The effects of cross and self-fertilization in the vegetable kingdom. New York, 1877. (p. 375.)

[23] Corry, T. H. loc. cit. 1883.

On bright sunny days a succession of many sorts of insects visit blooming plants of *Asclepias,* attracted by the showy flowers, their perfume, and particularly for the abundant nectar which is secreted by the hoods of their coronas. Prominent amongst these visitors are various Hymenoptera: the indigenous wasps and bees of the neighborhood.[*] Alighting upon an umbel of many flowers, each with five copious vessels of nectar, a bee or wasp will spend many minutes crawling or flying from one to the other and plunging its tongue greedily into each. As it sucks, it keeps up a characteristic movement of its barbed feet (pl. 1).

Delpino was able to observe, as a result of such movements, that a foot may by chance slide past the narrow space between the paired anther wings; and that if the motion continues to the top, a barb of the leg is virtually sure to wedge itself into the narrow vertical slit of the pollinium gland, attaching it almost inextricably. The wasps and bees, being strong insects, in dislodging their legs, easily pull the entire pollinium with its sacs of pollen from the broad apical pores of the anthers, and eventually fly on their way thus burdened. Weaker insects will perish in the trap or escape through loss of their limb.

Transfer of the pollinium sac to a stigmatic chamber is accomplished by the same casual movements of insects bearing the pollinia. Alighting upon a flower to

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[*] Our most extensive enumeration of insect pollinators of *Asclepias* was compiled by Charles Robertson (Trans. Acad. Sci. St Louis 5:569. 1891) over a period of 25 years. His data concerning seven species of *Asclepias* growing in the vicinity of Carlinville, Illinois, may be summarized as follows:

Asclepias verticillata:	Hymenoptera—27 genera, 38 species
	Diptera—11 genera, 13 species
	Lepidoptera—4 genera, 4 species
Asclepias incarnata:	Hymenoptera—21 genera, 41 species
	Diptera—10 genera, 15 species
	Lepidoptera—10 genera, 15 species
	Coleoptera—3 genera, 3 species
	Hemiptera—1 genus, 1 species
Asclepias syriaca:	Hymenoptera—13 genera, 14 species
	Diptera—10 genera, 11 species
	Lepidoptera—10 genera, 10 species
	Hemiptera—3 genera, 4 species
	Coleoptera—1 genus, 1 species
Asclepias sullivantii:	Hymenoptera—9 genera, 13 species
	Lepidoptera—4 genera, 4 species
	Coleoptera—1 genus, 1 species
	Diptera—1 genus, 1 species
Asclepias purpurascens:	Lepidoptera—4 genera, 5 species
	Hemiptera—1 genus, 1 species
	Hymenoptera—1 genus, 1 species
	Diptera—1 genus, 1 species
Asclepias tuberosa:	Lepidoptera—5 genera, 8 species
	Hymenoptera—5 genera, 6 species
	Diptera—1 genus, 1 species
Asclepias hirtella:	Hymenoptera—7 genera, 8 species
	Coleoptera—1 genus, 1 species

sip the nectar, a burdened leg sooner or later will slip a pollinium sac up the narrow space between the two contiguous anther wings. The size and shape of the stigmatic chamber and the pollinium sac of a given species of asclepiads are close counterparts, and the sac, fitting snugly into its destined chamber, breaks from its suspending translator arm as the insect leg continues upward, and remains lodged in close proximity to the receptive surface.

Not only the legs but any barbed or hairy surface of the insect's body is capable of dislodging and holding the glands of pollinia. As a result of his investigations, Robertson found pollinia carried by the claws, hairs of the legs, thorax, abdomen, and tongue, pulvilli, and spurs of the tibia. Since such emergences vary widely in diameter, it follows that they are adapted to a wide range of pollinia as determined by the slit of the gland within which they must be inserted. A single insect, therefore, may be capable of carrying simultaneously the pollinia of several species of *Asclepias*, and, in fact, repeatedly has been observed to do so.

Anther wings of *Asclepias* usually are very closely applied face to face except at one or two places: the very base, where a small open space remains in the angle of the two closely abutting margins, and at special notches or spurs indenting the wings and characteristic of certain species. At these open places the pollinium sac is introduced at the tip where it is constricted into a thin elbow-like joint with the translator arm, and is threaded upward into the stigmatic chamber by the movement of the insect's body. The attached gland of the pollinium remains outside the chamber. This is a feat which seems impossible to employ in hand pollinations, but it is in fact quite simple and far safer than trying to pry the wings apart with needles.

The feat is aided, in insect pollination, by a curious rotation of the translator arms through approximately 90°, doubtless due to drying and shrinking of the delicate membrane during the insect's flight. This torsion brings the pollinium sacs, which lie with their flat faces approximately perpendicular to the plane of the anther wings while they are still within the anther, to adopt a new position nearly parallel with the anther wings, *i.e.* with their narrow margin placed to insert between the wings with least resistance.

Pollinium sacs of *Asclepias*, as has previously been noted, are rather asymmetrically pyriform in shape. This is to say that the compressed margins are unequally biconvex. It happens, as was first noted by Brongniart[24], that when pollen tubes are produced from the germinating pollinia they issue from one place only: invariably at the more salient margin. This margin, certainly without accident, is that which corresponds to the inner contour of the stigmatic chamber and the point from which the tubes issue is brought mechanically into contact with the receptive surface of the stigma. This also is an additional device for the insertion of the pollinium sacs; for the salient margin will be that more easily introduced between the anther wings. In hand pollinations, also, one must obey this rule, and

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[24] Brongniart, A. T. loc. cit. 1831.

pollinium sacs inserted improperly, although likely to germinate regardless, will fail to make adequate contact with the stigma and thus fail in fertilization.

The fact that in pollination the pollinium sac only is lodged within the stigmatic chamber, leaving the gland and its translator arms attached to the insect, has a very curious consequence at times: for the tip of a free translator arm, when drawn up between the anther wings, is the correct thickness to become wedged within the slit of another pollinium gland, thus extricating its suspended pollinium sacs. This process can be repeated to produce an astonishing more or less regularly dichotomous "multiple pollinium", as it is called (pl. 1, inset). Corry once found a multiple pollinium consisting of eleven units.

Robertson observes that the multiplication of pollinia upon an insect's legs may have very serious consequences for the European hive bee in particular. The bee, fettered by the glands and translator arms, is seriously handicapped in its occupation of gathering pollen and nectar, and its clumsy movements in the hive result in its expulsion and death. My friend Bernard C. Mikula has shown me a hive bee with its legs encumbered by 45 pollinium glands and their attached translator arms.

It has been noted previously that the stigmatic chambers within which the pollinium sacs are deposited actually are composed of the lateral margins of the anthers themselves except at the very tip where a small area of the true stigma is exposed. For this reason the term "alar chamber", employed by some students of asclepiads including Corry, may be more appropriate morphologically. I prefer "stigmatic chamber" since it seems to emphasize the function more directly. It is interesting to find that stigmatic chambers, when ready for reception of the pollinium sacs, are obviously filled with a fluid resembling the nectar of the corona hoods. This secretion, interestingly, is not so much contributed by the receptive surface as by the anthers themselves, which here produce a very prominent glandular epidermis (pl. 3, fig. 1).

Pollinium sacs, when lodged within an actively secreting stigmatic chamber, promptly begin to absorb the secrete and to swell. Within two or three hours the salient margin in contact with the receptive surface ruptures and the pollen tubes start to emerge. When in contact with the stigma the tubes penetrate very quickly; they do not disperse during their growth, but assume the form of a cable or skein quite easily seen by the naked eye upon dissection, even when obtained from herbarium specimens. The cable of pollen tubes passes intact through the stigma head and style to the cavity of the carpel, where it emerges and disperses over the surface of the placenta, each tube seeking an ovule.

FRUIT:—

The fruit of *Asclepias* (fig. 3) is a simple dry follicle dehiscing along its ventral suture. The shape varies from nearly linear to very broadly ovoid and from about 2 dm. to only 3–4 cm. in length. The pericarp may be glabrous or variously pubescent and frequently is beset with more or less prominent fleshy spines in such species as *A. syriaca,*[25] *A. speciosa,* and *A. fruticosa.* A peculiar feature of certain

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[25] Further notes on variation in the pods of *A. syriaca* will be found in the taxonomic discussion of that species (p. 105).

Fig. 3. Types of fruit and seed of *Asclepias:* 1, *A. texana,* 2, *A. perennis,* 3, *A. subulata,* 4, *A. syriaca* (smooth fruit); 5, *A. syriaca* (spiny fruit).

fruits is the development of an inflated spongy endocarp which is particularly prominent in *A. viridis, A. asperula,* and the three species previously mentioned. This aerenchyma can best be observed in the fresh condition, since it collapses in desiccation; its function is quite problematic.

Although the two carpels of the gynoecium of *Asclepias* are equally developed at anthesis, it is exceedingly rare for both to develop fruit. One might suppose that the division of the receptive surface of the stigma amongst the five chambers might be a possible explanation since it is unusual for more than one or two chambers of a given flower to be pollinated successfully in nature. However, I have pollinated all five chambers of *A. curassavica* by hand, with the consequent production of solitary follicles. The cause, therefore, must be physiological rather than purely mechanical.

Similar physiological factors may be responsible for the surprisingly low ratio of fruit matured to the large number of flowers pollinated per plant. I have found that the species of the supposedly primitive series INCARNATAE, particularly *A. incarnata* itself, generally are the most fruitful, percentage-wise to the flowers per plant.

Many years ago I noted in various genera of the neighboring family Apocynaceae, where both carpels ordinarily mature fruit, that occasionally but one follicle develops or the pair may be more or less strongly unequal. This is particularly easy to observe in *Amsonia*. The converse situation in Asclepiadaceae may be a sequel to this trend, possibly destined to lead toward a monocarpellary gynoecium.

The hairs of the coma are smooth, extremely narrow, hollow tubes of practically pure cellulose, and possess astonishing buoyancy. The silky seed comas of species which grow in considerable colonies, such as *A. syriaca* and *A. incarnata*, were occasionally used as pillow stuffing by the early settlers. In World War II the U. S. Department of Agriculture undertook a rather extensive program to obtain large quantities of milkweed coma for the stuffing of life jackets; the program was conducted largely through the rural schools. The seed coma of *Calotropis*, a closely related genus, has been employed in paper making in southeastern Asia.

PHYLOGENY OF THE FRUIT:—

Phylogenetically, the most interesting aspect of the fruit of *Asclepias* is not the follicle itself but the accrescent pedicel which supports it. By far the greatest number of species of the tribe Asclepiadeae possess a most peculiar fruiting pedicel which, during its accrescence after pollination, produces a variable sigmoid curve; the follicle itself habitually is erect on such a pedicel, and is described in this text as "erect on deflexed pedicels." In other Asclepiadaceae the pedicels either are completely declinate, with the follicle pendulous, or erect with the follicle also erect.

In the genus *Asclepias*, although the greatest number of species produce follicles erect on deflexed pedicels as is characteristic of the tribe, a comparatively small number produce follicles erect on erect pedicels and still fewer with pendulous follicles as is customary for the family Asclepiadaceae generally. One might suppose the erect or pendulous fruiting pedicels to be a "primitive" character for the genus and the deflexed pedicels correspondingly "advanced."

In systematic studies of this sort, it obviously is highly desirable to correlate flowering and fruiting characters. I have striven to do so in *Asclepias*, although with only partial success. But the fact of evolution is demonstrated most clearly by the lack of complete correlation of characters in our systematic categories.

In the system for the North American species of *Asclepias* which is proposed here, the construction of the subgenera and series is made wholly on floral characters. This is necessary because of the many species involved and the great conservatism of the fruit. Since the fruit is so highly conservative, however, it provides a more reassuring guide, such as it is, to the phylogeny of the highly variable floral organs than would otherwise obtain.

It is probably reasonable to suppose that the follicles, erect on deflexed pedicels, are "advanced" phylogenetically since they are so unique to the tribe Asclepiadeae. Therefore those species of *Asclepias* having erect or pendulous fruiting pedicels, characteristic of the family Asclepiadaceae otherwise, might be considered "primitive." Upon these premises, the subgenus ASCLEPIAS might be considered as the most primitive not only from floral characters but from the fruit as well, since approximately one quarter of its species produce fruit with erect or pendulous pedicels; series INCARNATAE, considered the most primitive from floral structure, includes no species with deflexed fruiting pedicels and erect follicles.

Erect or pendulous fruiting pedicels are scattered throughout other subgenera as well as in other series of subgenus ASCLEPIAS, however; these species include *A. quadrifolia, A. viridula, A. pellucida,* and *A. pringlei* of ASCLEPIAS-SYRIACAE, *A. michauxii* of ASCLEPIAS-PURPURASCENTES, *A. labriformis, A. subaphylla, A. albicans,* and *A. masonii* of ASCLEPIAS-ROSEAE, *A. cinerea, A. feayi,* and *A. cutleri* of ASCLEPIODELLA, *A. stenophylla* of POLYOTUS, and *A. subulata* of PODOSTEMMA. In most instances, these species might well be considered "primitive" within their respective series and subgenera from the standpoint of floral morphology.

EVOLUTION

The elaborate pollinating devices of Asclepiadaceae might appear so exceptional amongst the Flowering Plants as to preclude direct comparison with any other family. However, Demeter[26] has succeeded in it by emphasizing certain undoubtedly significant trends in the neighboring Apocynaceae, also an entomophilous family. There the stigma head, which is far more variable in form than in Asclepiadaceae, also possesses an inferior stigmatic surface as a rule; there also the stigma produces a second secretion, which in this case is merely fluid and amorphous but of a consistency to facilitate transference of the granular pollen to the proboscides of visiting insects. Demeter probably is correct in interpreting the far more precise and specific translator apparatus of asclepiads as having arisen from such lower levels of organization; but I, and probably most other systematists, would not follow him in the consolidation of the two families in conclusion.

Although organs as highly developed as the corona of most Asclepiadaceae are not found amongst Apocynaceae, undoubtedly related structures exist in the more

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[26] Demeter, K. Vergleichende Asclepiadeenstudien. Flora n. s. 15:130. 1922.

or less conspicuous appendages of the staminal filaments of *Vallaris* and *Forsteronia* subgen. PTERANTHERA. In Apocynaceae nectar is provided by gynoecial disc structures, carpellodial in nature,[27] rather than by the staminal corona as in Asclepiadaceae. The diverse natures of the nectar-secreting organs serve to emphasize the systematic independence of the two families.

Schmalhausen's[28] principle of the evolutionary adaptation of animals according to their position in a hierarchy of nutrition has been supplemented by Stebbins,[29] who has proposed an adaptational classification of plants and of organs of plants according to three levels in a hierarchy of reproduction. According to Stebbins, the lowest level, in which evolutionary modification is slowest, includes those organisms and organs which rely solely upon a large number of gametes and zygotes and dissemination of them by air or water for the maintenance of their kind; the highest level, in which evolution is most rapid and diversification most extreme, includes particularly those plants with fewer diaspores, or their organs, which rely upon animals for pollination, seed dispersal, or both. Explaining this important truism by another, Stebbins concludes that "Since there are so many more diverse kinds of animals in any locality than there are different climatic or edaphic conditions, many more adaptive gene combinations are possible in plants which rely on animals for their vital reproductive functions."

Both the lowest and the highest of Stebbins' reproductive levels, and their ability to coexist within a single organism, are exemplified by the Asclepiadaceae with their conservative fruits and wind-borne seeds and their tremendously plastic entomophilous stamens. Speciation of *Asclepias* in North America having preoccupied my attention for a number of years past, I still am unable to identify more than fragments of the mechanisms which may be involved.

The genus *Asclepias* in North America, including the Antilles, consists of 108 species which have been distributed amongst nine subgenera. There is a noticeable, if irregular, tendency for the subgenera to decrease in number of species proportional to their supposed phyletic distance from the hypothetical ancestral plexus, subgenus ASCLEPIAS, which is by far the richest in species. Subgenus ASCLEPIAS, in turn, is subdivided into nine series amongst which there also is a tendency to diminish in number of species phyletically outward from the supposedly primitive series INCARNATAE.

An even more significant phenomenon, and one less likely either to individual subjectivity or to distortion by the linear sequence of pages, may quickly be perceived by an inspection of the flower drawings of each species provided in the taxonomic section which follows. Even a non-botanist can grasp the progressive compounding of floral complexity. What are the causes of the intricate canalization? Entomophily, alone, is an unsatisfying generality.

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[27] Woodson, R. E., Jr., and J. A. Moore. The vascular anatomy and comparative morphology of apocynaceous flowers. Bull. Torrey Bot. Club 65:135. 1938.

[28] Schmalhausen, I. I. Factors of evolution: the theory of stabilizing selection. Philadelphia, 1946.

[29] Stebbins, G. L., Jr. Rates of evolution in plants. Genetics, Paleontology, and Evolution. p. 229. Princeton University Press, 1949.

R. J. Moore,[30] in a cytogenetic study of several North American species of *Asclepias,* found all to be isoploid ($n = 11$), with the chromosomes small and relatively uniform in configuration, although those of *A. curassavica* were noticeably smaller than the rest (which may support our impression that that species is not indigenous to North America). He also attempted various artificial hybridizations involving six species, all without success. To Moore's list of unsuccessful pollinations I can add the following:

curassavica × *quadrifolia,* and reciprocal
curassavica × *purpurascens*
**fascicularis* × *verticillata,* and *reciprocal
**fascicularis* × *incarnata*
**verticillata* × *incarnata*
angustifolia × *curassavica*
**angustifolia* × *verticillata*

Ten flowers were pollinated for each. Those preceded by an asterisk were followed by production of small fruit which failed to mature. I was surprised and rather disappointed that those of the list asterisked failed to mature fruit; for all are apparently closely allied species of my "primitive" series INCARNATAE.

O. A. Stevens[31] reports successful artificial hybrids of *A. speciosa* × *A. syriaca* after many attempts, and several botanists have collected supposed natural hybrids of the same species. I have seen several herbarium specimens supporting these reports. Aside from these, I do not believe that I have encountered many more than a dozen plants that I would construe as interspecific hybrids amongst the thousands of specimens of the 73 species of the United States that I have examined, either in the herbarium or in the field. The incidence appears to be only slightly higher in Mexico.

A list of apparently interspecific hybrids which I have examined in the herbarium, and their distribution amongst the subgenera and series of this revision follows. Some items are rather indefinite and open to interpretations other than hybridity.

pumila × *verticillata* (both species ASCLEPIAS-INCARNATAE)
Plants branching copiously toward the crown, rather as in *pumila;* leaves linear, broader and longer than normally in either species, irregularly opposite, spiral, or ternate, with internodes longer than in either species; corona hoods entire.—Leeds, North Dakota, July 20, 1913. *J. Lunell* (MO).

coulteri × *quinquedentata* (both species ASCLEPIAS-EXALTATAE)
Discussed in the taxonomic section under *A. coulteri.*

amplexicaulis × *humistrata* (ASCLEPIAS-EXALTATAE; ASCLEPIAS-SYRIACAE)
Plants simulating *amplexicaulis,* but less erect and with tendency to lateral, more shortly pedunculate inflorescences in the upper leaf axils; flowers with shorter columns and shorter, less cylindrical hoods than in *amplexicaulis.*—Aspalaga, Florida, May, 1898, *A. W. Chapman* (MO).

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[30] Moore, R. J. Investigations on rubber-bearing plants. IV. Cytogenetic studies in *Asclepias* (Tourn.) L. Canad. Jour. Res. 24C:66. 1946.

[31] Stevens, O. A. The cultivation of milkweed. N. Dak. Agr. Exp. Sta. Tech. Bull. 333. 1945.

amplexicaulis × ***syriaca*** (ASCLEPIAS-EXALTATAE; ASCLEPIAS-SYRIACAE)

Plants probably involving such hybridization have been described by Miss Vail as follows:

Asclepias bicknellii Vail, in Bull. Torrey Bot. Club 31:458. *pl. 19.* 1904. Leaves crisped as in *amplexicaulis;* flowers intermediate, with shorter column than in *amplexicaulis,* hoods truncate and slightly erose as in *amplexicaulis,* but of thinner texture as in *syriaca.*—Van Cortlandt Park, New York City, June 25, 1895, *E. P. Bicknell* (NY).

Asclepias intermedia Vail, loc. cit. 459. *pl. 16.* 1904. Leaves pubescent as in *syriaca* but somewhat crisped as in *amplexicaulis,* umbels shortly pedunculate as in *syriaca;* flowers intermediate but somewhat more like *syriaca* (slightly longer column, more sharply ascending and larger hoods). Lawrence, Long Island, July 17, 1904, *E. P. Bicknell* (NY).

syriaca × ***viridiflora*** (ASCLEPIAS-SYRIACAE; ACERATES)

Plants pubescent, with leaves rather small for *syriaca;* inflorescence solitary, subterminal; flowers strikingly intermediate, of intermediate size, column nearly obsolete, hoods nearly erect, narrow, somewhat saccate at the base, slightly longer than the anther head, with inconspicuous marginal auricles, no horn; pollinia intermediate, conspicuously attenuate.—Long Point, Lake Maxinkuckee, Marshall County, Indiana, August 26, 1926, *J. R. Churchill* (MO).

speciosa × ***syriaca*** (ASCLEPIAS-PURPURASCENTES; ASCLEPIAS-SYRIACAE)

The general habit of both putative parents is closely similar; flowers of the putative hybrids are intermediate in size and degree of attenuation of the hoods. This hybrid has been created experimentally by O. A. Stevens, and is encountered in the field in northwestern Iowa and adjacent Minnesota and North Dakota.—Ruthven, Iowa, July 26, 1943, *A. Hayden 3145* (MO).

lanuginosa × ***pringlei*** (ASCLEPIAS-PURPURASCENTES; ASCLEPIAS-SYRIACAE)

Discussed in the taxonomic section under *A. lanuginosa.*

emoryi × ***oenotheroides*** (both species PODOSTEMMA)

Discussed in the taxonomic section under *A. emoryi.*

elata × ***glaucescens*** (ASCLEPIODORA; ASCLEPIAS-GRANDIFLORAE)

Discussed in the taxonomic section under *A. elata.*

This list is remarkably meagre considering the size of the genus *Asclepias* in North America, in contrast to my previous experience with the systematics of Flowering Plants. Although more extensive cytogenetic evidence certainly is necessary, I believe it probable that neither polyploidy nor hybridization has played a significant part in the speciation of *Asclepias* in this area.

The pollinating apparatus of asclepiads is so elegantly contrived that it has been only natural to ascribe to it the relative purity of their species. It has been quoted widely as one of the most outstanding examples of mechanical isolation in plants, and I myself have held this view. More recently the evidence for this assumption has seemed less compelling to me.

One is apt to associate constancy with such structural intricacy as one sees in the flowers of *Asclepias.* Nevertheless, considerable variation is found, and one must not consider the flower drawings accompanying this revision, for example, as inviolable patterns from which all individuals of a species are cast. I have gathered statistical data for such variation with respect to only two structures of a single species, *A. tuberosa,* where the hood length has the astonishingly wide colonial range in values for V of 0.4 to 6.6 in Iowa and Minnesota, the data obtained from local population samples. Pooled measurements of the pollinium sac length of the same species in its midwestern range, obtained from herbarium specimens, yielded a value for V of 1.7.

Such variability as that of pollinium sac length bespeaks the probability of similar variability in the dimensions of the stigmatic chamber and casts doubt on the lock-and-key simile which has been coined for the pollinating apparatus of *Asclepias.* Surely such a large pollinium sac as that of *A. erosa* could scarcely be accommodated within the far smaller stigmatic chamber of *A. fascicularis,* for example; yet my friend Dr. R. W. Holm informs me that he has found the smaller pollinium sacs of *A. fascicularis* lodged and germinated within the larger stigmatic chambers of *A. erosa.*

Both R. J. Moore[32] and I have found all species which we have pollinated to be self-sterile. Plotnikova[33] and O. A Stevens[34] have reported *A. syriaca* to be capable of self-pollination, but Moore, who has made a thorough investigation of the claim, considers it unlikely; similarly, Fischer[35] asserts that *A. incarnata* may be self-fertile, but that has not been my experience. It should be possible, therefore, to place single potted plants of *Asclepias* side by side, removed from other plants of the same species and available to insect pollinators, in order to observe whether pollinia of one are able to be lodged within the stigmatic chambers of the other through natural means. I have done this with potted plants of *A. fascicularis* and *A. verticillata,* and small abortive pods have been produced similar to those obtained through artificial cross pollination. The barriers separating these species apparently are physiological and not mechanical.

Nor are the insect pollinators limited to certain species of *Asclepias,* exclusive of physical strength to withdraw the larger pollinia. The extensive observations of Robertson,[36] already quoted, have shown numerous genera and orders of insects transporting the pollinia of a given asclepiad, as well as the transportation simultaneously of pollinia from diverse asclepiads by the same pollinator.

I am more inclined to view the physiological barriers as primary in maintaining the genetic purity of the species of *Asclepias.* Equally, after their origin through mutation, physiological barriers might construct a reservoir damming the flow of genes affecting various structures and launching a new morphological species in time, natural selection permitting. Mechanical isolation of numerous asclepiad species there doubtless is, but I feel that it is secondary and the product of the primary processes of physiological isolation and mutation.

Could not such a mechanism of speciation which is envisioned produce the gradually diverging floral innovations at which we marvel? It appears to me quite more than likely that the series, and perhaps even the subgenera, of this revision are unnatural in the sense of common horizontal levels of development attained more or less fortuitously by species of independent radiating lines of descent. Is this not suggested by our list of putative hybrids, in which species of different series or even subgenera are so frequently involved? The lines themselves are too subtile for description or even for perception, and one must satisfy himself with analogies.

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[32] Moore, R. J. loc. cit. 1946.

[33] Plotnikova, T. An experiment in self-pollination of *Asclepias cornuti.* Ukraine Acad. Sci., Inst. Bot. Jour. No. 26–27:127. (English summary).

[34] Stevens, O. A. loc. cit. 1945.

[35] Fischer, E. Der Anbau einer Faser- und Bienenfutterpflanze. Pflanzenbau 17:212. 1941.

[36] Robertson, C. Notes on the mode of pollination of *Asclepias.* Bot. Gaz. 11:262. 1886; Insect relations of certain Asclepiads. I. Bot. Gaz. 12:207. 1887; II. loc. cit. 244. 1887; Flowers and insects, Asclepiadaceae to Scrophulariaceae. Trans. Acad. Sci. St. Louis 5:569. 1891.

The North American species of *Asclepias* form a coherent alliance amongst themselves quite independent of those indigenous either to Africa or to South America. The three centers appear merely as individual segments of the radiating phylogeny to which I have alluded. It is obvious that both the African and the South American segments include in part much the same type of floral modification as that which I include within my subgenus ASCLEPIAS series INCARNATAE and which I construe to be the primitive element in North America. The South American, with its few species, has not progressed far beyond this supposedly primitive level of modification. The African, however, has spread into quite as labyrinthine paths of floral diversification as has the North American and frequently with closely parallel development. But I cannot share the recent view of Bullock[37] that the name *Asclepias* must be confined to America. All that one may say, I believe, is that the American species usually have a horn accompanying the corona hoods and the African do not. That species groups of a genus have been separated for ages and so have developed independently of necessity entitles them no more to rank as individual genera than would be the case with similarly isolated species.

Systematic Levels:—

I have discussed my reasons for adopting an ultra-conservative interpretation of the genus *Asclepias* in the first paper[38] of this series. Chief amongst these is the nearly continuous variation of the floral characters which have been used as the basis for generic segregations. This will be perceived readily in the drawings which accompany the taxonomic section which follows, and is reflected by the divergent treatment of genera, even from nearly identical areas, in such standard and strictly contemporaneous works as the second edition of Britton and Brown's 'Illustrated Flora'[39] and the eighth edition of 'Gray's Manual'.[40]

The subgenera as employed here, follow in general the amplified boundaries of several of the segregate genera of floristic manuals, although a few have had to be suppressed completely largely for the sake of intelligibility in the keys; a few previously neglected segregate genera, such as Nuttall's *Polyotus* and Greene's *Podostemma*, have been revived to the degree of subgenera for reasons of systematic balance. The several series of the subgenus ASCLEPIAS reflect the considerable variation of this large assemblage of species. As discussed previously, I believe them to be "horizontal" sequences phylogenetically, at least in part, in the sense of being common levels of modification attained perhaps independently by several parallel lines of evolutionary development—and unnatural to that extent. Series INCARNATAE, however, I consider to be "natural", or more nearly so, in the usual sense of the term.

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[37] Bullock, A. A. Notes on African Asclepiadaceae, I. Kew Bull. 1952:426. 1952.

[38] Woodson, R. E., Jr. The North American Asclepiadaceae, I. Perspective of the genera. Ann. Missouri Bot. Gard. 28:193. 1941.

[39] Gleason, H. A. The new Britton and Brown illustrated flora. vol. 3, p. 73. Lancaster, Penn., 1952.

[40] Fernald, M. L. Gray's manual of botany, ed. 8. p. 1169. New York, etc., 1950.

Species are the most fundamental of systematic populations. It thus appears only just to require of them a definite morphological character in addition to genetic cohesion. Every systematist knows that no two species, even of a single genus, are exactly equivalent either in the sum of their morphological characters or in their variability, although that is the ideal toward which our methods aspire. The ideal is practical in so far as it is pursued conscientiously and its limitations are recognized.

In this treatment, the species of *Asclepias* are of quite unequal value morphologically. As has been intimated previously, the species of the supposedly primitive series INCARNATAE of subgenus ASCLEPIAS are scarcely distinguishable upon the basis of floral structure; the differences are based upon vegetative characters and fruit as a rule. In the higher series and subgenera, on the other hand, species differences are mostly floral and increase rather constantly in complexity to the most advanced subgenera.

The pronounced physiological and mechanical barriers between the North American species of *Asclepias* are an invaluable aid in the definition of the species as a systematic unit. Interspecific hybrids, as has been discussed previously, are either unknown or of more or less sporadic occurrence. Geographically distinguished races of some definite morphological character which are connected by obvious clines of apparently heterozygous populations are classified as subspecies. The genocline is the distinguishing criterion. Here again the subspecies are of unequal morphological value. Such subspecies as those of *A. incarnata* and *A. tuberosa,* being of relatively "primitive" series, are distinguished upon chiefly vegetative characters, while others of more "advanced" series, such as *A. cryptoceras* and *A. californica,* are characterized by floral structures which might be considered as of specific value in the absence of evidence of a genocline.

Although subspecies are allopatric by definition, an apparent exception is found in *A. tuberosa* sspp. *interior* and *terminalis,* a preliminary study of which has been published in another journal.[41]

In a few species more or less pronounced variation of various organs, such as the leaves in *A. viridifolia,* display no geographic or ecological pattern. These frequently have been made the basis of "varieties" in the past. In this treatment such variation is suspected as evidence of neutral polymorphism and is ignored systematically.

GEOGRAPHY

The species of the inclusive genus *Asclepias* are distributed amongst three centers of dispersal: temperate to tropical North America, subtropical South America, and southern and eastern Africa. Of these, the North American and the African are by far the largest, including over a hundred species apiece. The South American, notably isolated by approximately 3,000 miles from the larger center to the

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[41] Woodson, R. E., Jr. Biometric evidence of natural selection in *Asclepias tuberosa.* Proc. Nat. Acad. Sci. 39:74. 1953.

north, appears to consist of less than a dozen poorly differentiated species. None is indigenous to more than one of these centers; but the American *A. curassavica* is widespread in the tropics and subtropics of both hemispheres as an escape from cultivation, and the African *A. fruticosa* appears sporadically as a waif in tropical America, Hawaii, and perhaps elsewhere.

The North American species of *Asclepias* are adapted to a wide range of environment. Being essentially subtropical plants, their altitudinal and latitudinal preferences are somewhat restricted; few extend to elevations over 2,000 meters, and only few cross the southern borders of the Canadian provinces. The individual species actually are rather narrow in their ecologic preference, and only *A. syriaca, A. curassavica,* and *A. fasciculata* (and possibly *A. incarnata*) can be classified as weeds. Most species prefer rather open dryish woods, glades, barrens, and plains.

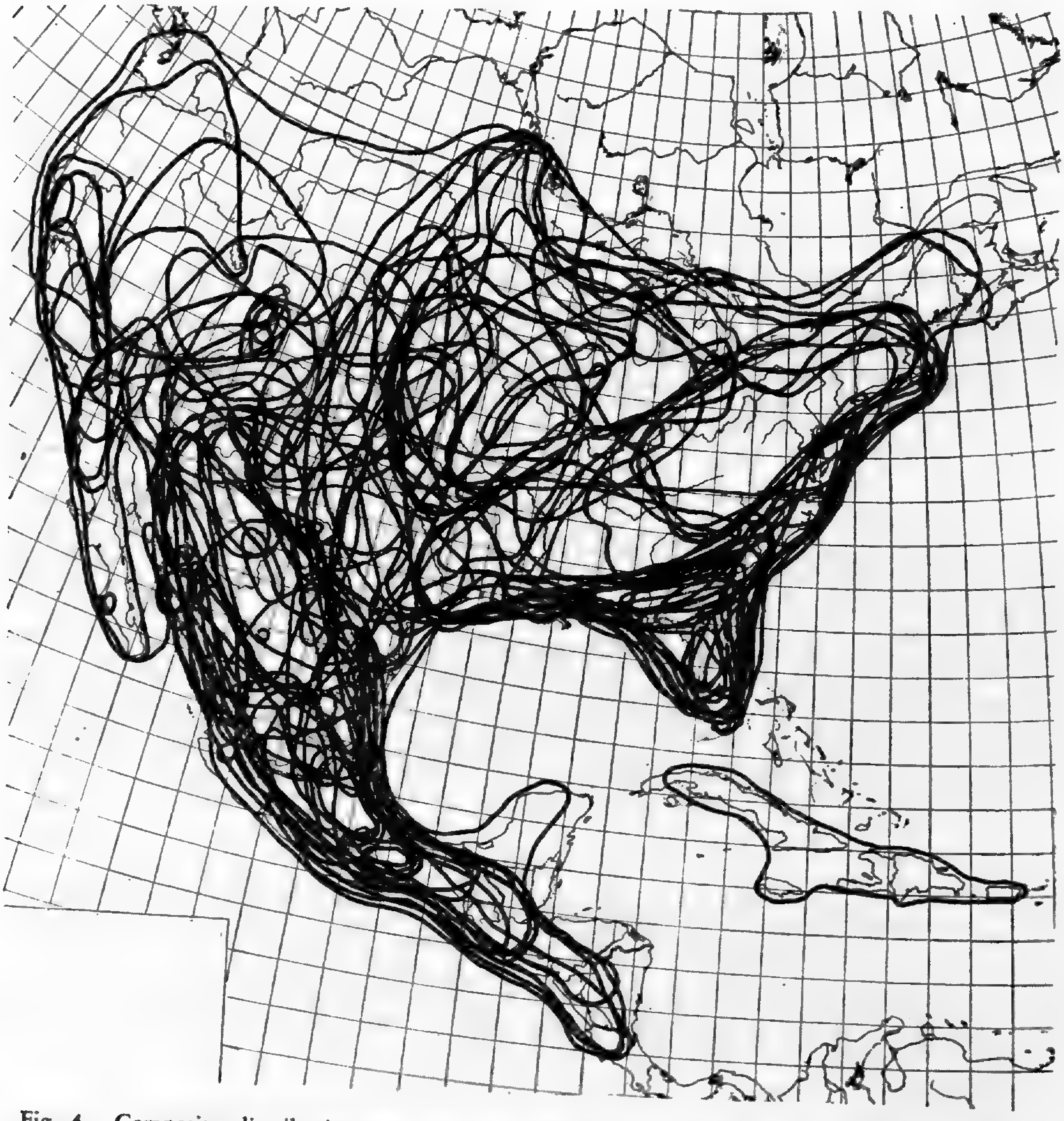

Fig. 4. Composite distribution map of 106 indigenous North American species of *Asclepias.* Explanation in the text.

Several desert species are found in the southwestern United States and adjacent Mexico and these frequently adopt strikingly similar twiggy, *Ephedra*-like habits with narrow fugaceous foliage. Only *A. perennis* and *A. incarnata* are subaquatics; *A. i. pulchra* is outstanding in its tolerance of more or less brackish water.

If the distribution maps provided for each of the 106 indigenous species in the taxonomic section which follows are generalized as closed loops and drawn upon a single map of North America, the resulting confusion well depicts the complexity of the geography of *Asclepias* upon this continent. However, it appears to me that six vortices or centers of concentration may be distinguished (fig. 4) which I call, from southeast to west, the Antillean, the Floridian, the Appalachian, the Ozarkian, the Mexican, and the Californian.

I have assigned the indigenous species of *Asclepias* to one (sometimes to two or three) of the six centers of concentration as indicated in Table I. Vicarious subspecies of a common species are tabulated in the same manner as for species, and the waifs, *A. curassavica* and *A. fruticosa*, are eliminated completely.

Many loops necessarily converge at the coast line (and unfortunately beyond!), but more significant from our standpoint are the convergences within the continent, since these indicate the complementary bounds of the species: they are similar to the lines upon a contour map. It is obvious that relatively few distributions of any center (the Antillean consists of but one!) are exactly equiformal, but the centers possess reality none the less in the sense of statistical tendencies. Discussion of a few distributions chosen from the eastern United States will illustrate not only the method of compilation but also certain important factors in the distribution of *Asclepias* in this area and in general.

Asclepias tuberosa, which consists of four subspecies, may form the basis of discussion since more is known of its geography than of any other species.[42, 43] The distribution of this species is illustrated by the upper left panel of fig. 5. The four subspecies are distinguished chiefly on leaf shape which, while relatively constant within the respective centers of distribution, intergrade at the juncture of the ranges with so greatly increased accompanying variation as to be clearly indicative of hybridization.

As I have pointed out in an earlier discussion of the distribution of *Asclepias* in the eastern United States,[44] the areas occupied by the subspecies of *A. tuberosa* correspond closely to three well-known floristic and paleogeographic regions, namely, Appalachia, Ozarkia, and the Floridian "Orange Island"; and the familiar geographic isolation of the three, determined by incursions of the sea and glaciation in the Cretaceous and the Cenozoic times, might logically be assumed as contributory to the evolution of their respective subspecies. It will be noticed, however,

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[42] Woodson, R. E., Jr. Some dynamics of leaf variation in *Asclepias tuberosa*. Ann. Missouri Bot. Gard. 34:353. 1947.

[43] Woodson, R. E., Jr. Biometric evidence of natural selection in *Asclepias tuberosa*. Proc. Nat. Acad. Sci. 39:74. 1953.

[44] Woodson, R. E., Jr. Notes on the "historical factor" in plant geography. Contr. Gray Herb. Harvard Univ. 165:12. 1947.

TABLE I

THE INDIGENOUS NORTH AMERICAN SPECIES OF *ASCLEPIAS CORRELATED* SYSTEMATICALLY WITH REGARD TO THE SIX GEOGRAPHICAL CENTERS OF CONCENTRATION. EXPLANATION IN THE TEXT.

	Subgenera and Series	Appalachian	Ozarkian	Floridian	Mexican	Californian	Antillea
ASCLEPIAS	INCARNATAE	1b *incarnata pulchra* 3 *perennis* 13 *verticillata*	1a *incarnata incarnata* 13 *verticillata* 14 *pumila*	13 *verticillata*	2 *texana* 4 *woodsoniana* 5 *linearis* 6 *pseudorubricaulis* 9 *angustifolia* 11 *subverticillata* 12 *mexicana* 15 *leptopus* 16 *gentryi*	10 *fascicularis*	8 *nivea*
	TUBEROSAE	17a *tuberosa tuberosa* 18 *rubra*	17c *tuberosa interior* 17d *tuberosa terminalis*	17b *tuberosa rolfsii* 19 *lanceolata*			
	EXALTATAE	23 *exaltata* 26 *amplexicaulis*	26 *amplexicaulis*		20 *ovata* 21 *similis* 22 *contrayerba* 24 *coulteri* 25 *quinquedentata* 27 *virletii* 28 *scaposa*		
	GRANDIFLORAE				29 *crocea* 30 *grandiflora* 31 *glaucescens*		
	SYRIACAE	32 *quadrifolia* 36 *syriaca*	32 *quadrifolia* 35 *ovalifolia* 36 *syriaca* 38 *meadii*	33 *viridula* 37 *humistrata*	34 *pellucida* 39 *hypoleuca* 40 *pringlei* 41 *pratensis* 42 *linaria*		
	PURPURASCENTES	44 *variegata* 45 *purpurascens*	43 *sullivantii* 45 *purpurascens*	48 *curtissii*	46 *ballii* 47 *lanuginosa* 49 *speciosa* 50 *euphorbiaefolia*		

TABLE I (Continued)

ASCLEPIAS	MACROTIDES			51 *michauxii*	52 *conzattii* 53 *involucrata* 54 *macrosperma* 55 *puberula* 56 *macrotis* 57 *lemmonii* 58 *laxiflora*		
	ROSEAE			59 *tomentosa* 62 *obovata*	60 *arenaria* 61 *latifolia* 63 *labriformis* 67 *subaphylla* 70 *nummularia* 71 *rosea*	64 *erosa* 65 *eriocarpa* 66 *masonii* 68 *albicans* 69 *vestita*	
PODOSTEMMA					73 *auriculata* 75 *nyctaginifolia* 76 *oenotheroides* 77 *emoryi* 78 *standleyi*	74 *subulata*	
ANANTHERIX				79 *connivens*			
ASCLEPIODELLA				80 *cinerea* 81 *feayi*	82 *brachystephana* 83 *ruthiae* 84 *cutleri* 85 *uncialis*	86 *cordifolia*	
ACERATES		90 *viridiflora*	88 *hirtella* 90 *viridiflora* 91 *nuttalliana*	89 *longifolia*	87 *vinosa*		
SOLANOA					93 *cryptoceras*	92 *californica* 94 *solanoana*	
POLYOTUS			95 *stenophylla*		96 *rusbyi* 97 *engelmanniana*		
ASCLEPIODORA		103 *viridis*	103 *viridis*	103 *viridis*	98 *elata* 99 *mirifica* 100 *fournieri* 101 *zanthodacryon* 102 *sperryi* 104 *asperula*		
PODOSTIGMA				107 *pedicellata*	105 *circinalis* 106 *atroviolacea*		

that not one, but two subspecies of *A. tuberosa* are classified as Ozarkian, namely, *terminalis* and *interior.* The anomaly of the distributions of these is the obvious fact that they are concentric to one another throughout their vast ranges: *interior* occupies a central core with a diameter roughly equivalent to the distance from southern Michigan to central Texas, and *terminalis* a concentric peripheral arc from southern Ontario to Sonora. Rather extensive biometric studies[45] which are not yet complete strongly imply that both subspecies have had their origin in the Ozark plateau, *terminalis* being the older, and that *interior,* a more recent genetic innovation within the former, is in the process of diffusing through the range of the parent subspecies and of supplanting it by virtue of certain traits (viz. increased reproductive potential, greater vegetative vigor) of obvious selective superiority.

It is demonstrable biometrically[46] that the diffusion of ssp. *interior* into glaciated and unglaciated areas has been remarkably symmetrical. It appears justified, therefore, to conclude that the origin of *interior* must date long since the retreat of Wisconsin glaciation in late Pleistocene, since *terminalis* has preceded it into glaciated territory.

Origin through spatial isolation has become such a keystone to the definition of subspecies that the theory of the sympatric origin of subspecies *terminalis* and *interior* doubtless will not be acceptable to some present-day evolutionists. On the other hand, I doubt that many would deny the transformation of populations *in situ,* since such an attractive theory as that of Sewall Wright's genetic drift is implicit in it and since the alternative would impute a rigidity of populations in space and time which would generally be recognized as erroneous. I am not personally familiar with more compelling evidence amongst plants of the gradual genetic transformation of populations through mutation and natural selection essential to the modern doctrine of evolution, nor upon a grander scale than that afforded by *A. tuberosa* sspp. *terminalis* and *interior.* To withhold systematic recognition to two such contending populations would defeat both of the primary functions of systematics: precision of reference and phylogenetic depiction.

Fortunately, no apologies are necessary for subspecies *tuberosa* and *rolfsii,* which clearly are allopatric. However, the approximate dating of *tuberosa, terminalis,* and *rolfsii* is more difficult than for *interior.* It is familiar knowledge that the Appalachian and Ozark plateaus have been available continuously for colonization by land plants since Paleozoic. Since Late Mesozoic, when angiosperms attained their ascendency, Appalachia and Ozarkia have been separated to the south by the Mississippi embayment of the Cretaceous seas and later by the delta sediments deposited in it. During the extensive glaciation of early Pleistocene, Appalachia and Ozarkia were disjunct from the north while still separated from the south ecologically, at least as far as non-alluvial plants are concerned (which includes by far the majority of asclepiads). Within these disjunct areas *A. t. tuberosa* and

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[45] Woodson, R. E., Jr. loc. cit. 1953.

[46] Woodson, R. E., Jr. Some dynamics of leaf variation in *Asclepias tuberosa.* Ann. Missouri Bot. Gard. 34:353. 1947.

terminalis may well have had their inception. Similarly, the less familiar fluctuating Floridian archipelago known as "Orange Island",[47, 48] for which there is stratographic evidence since the Cretaceous, may be considered a possible refugium for ssp. *rolfsii* with considerable justification.

Although it surely would not be justified to conclude that *A. tuberosa* existed in Cretaceous in exactly the form as it is known today, it appeals to me entirely defensible to conclude a common ancestor of our four present-day subspecies, and of not too different form. Perhaps Miocene would serve as a rough approximation of the time of their divergence as subspecies.

Finally, it appears to me significant that the obviously youngest subspecies of *A. tuberosa*, ssp. *interior*, can safely be considered as having arisen in the ancestral refugium of Ozarkia, in spite of the wide range of climatic and edaphic conditions offered by the vast distribution of the parent subspecies *terminalis*. That this is a general phenomenon in *Asclepias* is attested by the tendency of the species distributions, as shown in fig. 4, to converge over the six centers of concentration to which attention was drawn in previous paragraphs. I hold the opinion that this tendency is the direct product of the age of the refugium and the mutation rate of the populations concerned: that, in general, the longer an area is inhabited by a population, the greater the opportunity for favorable mutations to arise within it. This of course has nothing to do with the varying opportunities for adaptive radiation offered by the nature of the refugium.

While I hold the foregoing historical factor to be primary in interpreting the distribution of *Asclepias* in eastern North America, the role of adaptation to environment is closely involved as well. The ecologic complex of a refugium may gradually change to the disadvantage of an inhabiting population to the end that the latter may be obliged to shift its distribution to one more favorable, if available through its instruments of dispersal; or, failing that, may decline and be supplanted by another population of greater adaptive value by whatever means. Or a population actually may become preadapted to an area other than its original one and may spread to it if available, partially or wholly removing from its original site. Lastly, although the ecologic complex of a refugium may change in certain critical respects, in many cases the population may be expected to be sufficiently plastic with regard to its tolerance to adjust to its environment and so continue to inhabit it. I feel that these opinions are in general harmony with those of Good,[49, 50] the leading proponent of the theory of tolerance in plant geography, although certainly less so with those of such extreme adaptationists as Mason.[51] The following examples will illustrate my position.

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[47] Vaughan, T. W. A contribution to the geologic history of the Floridian plateau. Carnegie Inst. Wash. Publ. 133:99. 1910.

[48] Campbell, R. B. (quoted by R. E. Woodson, Jr.) Contr. Gray Herb. Harvard Univ. 165:12, 1947.

[49] Good, R. A theory of plant geography. New Phytologist 30:149. 1931.

[50] Good, R. The geography of flowering plants. Chap. 21. London & Colchester, 1947.

[51] Mason, H. L. The edaphic factor in narrow endemism. I. The nature of environmental influences. Madroño 8:209. 1946.

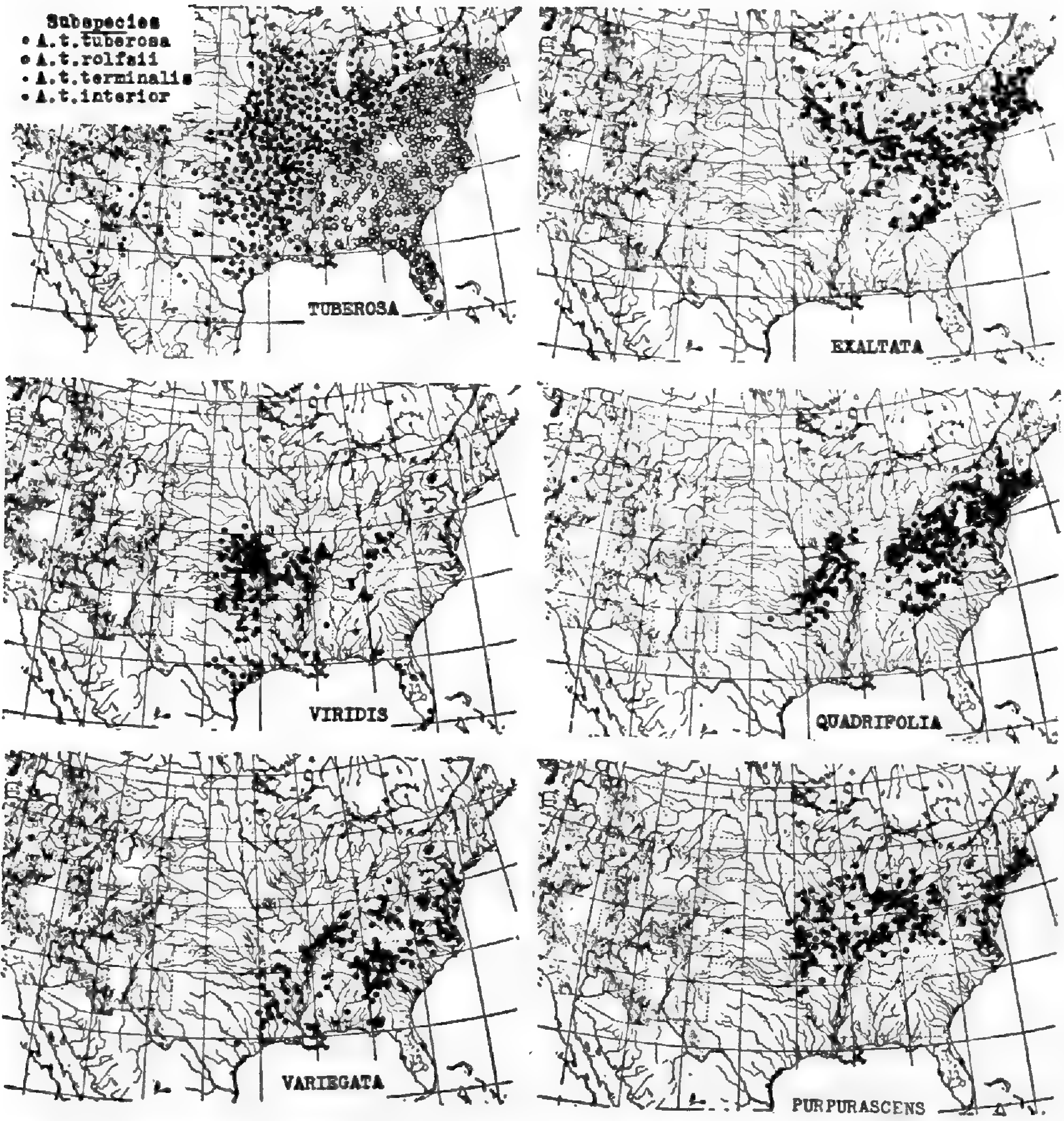

Fig. 5. Geographical distribution of six species of *Asclepias*. Explanation in the text.

The distribution of *Asclepias viridis* (fig. 5, middle left panel) is peculiar in its frequency on glades and prairies west of the Mississippi and south of the Missouri, and its relative rarity on the western slopes of the Appalachians and in Florida. Few known stations intervene. Plants of the three populations are indistinguishable to me. It seems to be that the range of *A. viridis*, as for *A. tuberosa*, is tricentric and probably of great age, but that subspeciation has not proceeded as in the latter. The Ozark representation appears obviously better adjusted to its environment than either the Appalachian or the Floridian which, in fact, appear poorly adjusted and in decline.[52] It is remarkable that the species has but barely crossed into glaciated

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[52] Dr. E. Lucy Braun (to whom I had shown my manuscript) comments: "This species, in southern Ohio, occurs in habitats quite comparable to the glades of Missouri. It is sometimes very abundant and aggressive, spreading onto eroded slopes of poor pastures (from more natural prairie communities) where the plants are very large. The largest number are on slopes of Crab Orchard Shale, a sticky calcareous shale (Silurian). They are well adjusted to their environment, and I would not say that the species (in Adams County, at least) is on the decline, although its habitat is being lessened in extent because of closing-in of secondary woodlands, and cultivation."

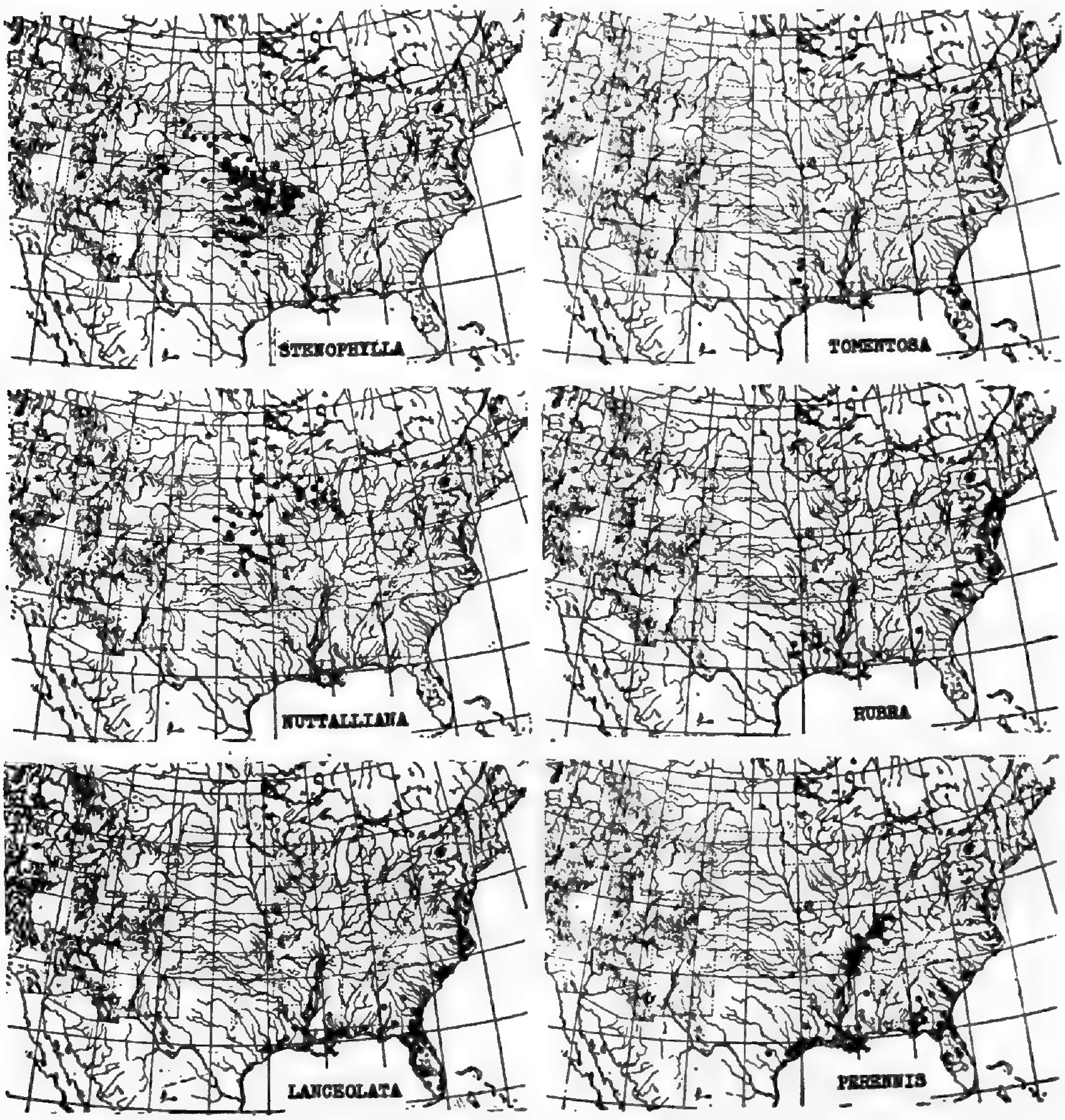

Fig. 6. Geographical distribution of six species of *Asclepias*. Explanation in the text.

areas, again unlike *A. tuberosa* with which it is characteristically associated ecologically in their common area. It has, however, populated such higher areas of the Mississippi embayment as Crowley's Ridge in Arkansas and southeastern Missouri and the Tupelo Hills in eastern Louisiana.

Asclepias variegata (fig. 5, lower left panel) is a species of thickets and open woods, usually in sandy or rocky soil. It obviously is an Appalachian species and monocentric. It is notable in its rather symmetrical adaptation to the varying ecological complexes of the high Appalachians of the Carolinas, Tennessee, and Georgia, the coastal lowlands from New Jersey to eastern Texas, and the southern Mississippi-Ohio lowlands. The emergence of ecotypes may be foreshadowed by local concentration of stations in various areas, particularly the southern Appalachian highlands and the Mississippi-Ohio lowlands.

The interesting distribution of *A. exaltata* (fig. 5) would be described as typically northeastern by some geographers since it lies predominantly within glaciated territory; they would interpret such a species as extending into the highlands of the southern Appalachians perhaps from nunataks in the north. I would interpret the data conversely: that being preadapted to the moist woods, meadows, and copses of the northeast, *A. exaltata* has proceeded to migrate into them from its ancient refugium in the southern Appalachians.

The bicentric distribution of *A. quadrifolia* (fig. 5) is exceptionally clear because of the disjunction of the Appalachian and Ozark populations. The species generally frequents rather dry and rocky woods and thickets, and the lower Mississippi lowlands and the prairies of Illinois and adjacent Indiana may be insuperable to the union of the eastern and western populations. Since the available habitats of the Ozarks are distinctly drier than those of the Appalachians, particularly to the north, an ecotypic response may have been evoked. Morphologically, however, I have found the two populations to be indistinguishable, contrary to expectation. The disjunction must be of very great antiquity.

Asclepias purpurascens (fig. 5), like *A. quadrifolia,* apparently consists of two disjunct populations which I would refer to Ozarkia and Appalachia as well. The species is unusually wide in its ecologic tolerance, frequenting thickets and open woods, prairies and fields, often escaping to roadsides and railway embankments. Unlike *A. quadrifolia,* however, here it is the Ozark population which is the larger, spreading from the Iowa prairies to the southern Great Lakes and to the western slopes of the Appalachians themselves. The Appalachian population proper, however, has withdrawn almost completely from its putative refugium to the middle and northern Atlantic coast.

The distribution of *A. stenophylla* (fig. 6) surely is Ozarkian; but from the western Ozarks, chiefly west of the Gasconade River, the species has fanned out into the plains of Kansas, Nebraska, Oklahoma, and adjoining margins of neighboring states. It would appear to have been preadapted to a plains environment because of an early occupance upon the semi-xerophytic "bald-knobs" of the Ozarks; an environment, incidentally, which presently is being diminished by the encroaching forests. *Asclepias stenophylla* apparently is in the act of moving out from its ancestral home.

Asclepias nuttalliana (fig. 6) is the northernmost of the species of subgen. ACERATES, the remaining species of which (with the exception of the enigmatic Mexican *A. vinosa*) are clearly referable to the Ozarkian, the Appalachian, or the Floridian centers of concentration. The distribution of the species lies in a great arc from Lake Michigan to southern Kansas; from the northern prairies to the eastern Great Plains. The focus of the arc converges almost directly upon the Ozark plateau, the refuge from which I believe that it, or its immediate ancestors, departed not long since, in terms of the history of the genus, *i.e.* subsequent to Pleistocene. I cannot suggest a simpler or more direct conclusion.

Distributions of the southeastern coastal plain involve inherent difficulties. Although stratographic geology, the impressive number of endemics, and such population dynamics as those of *Asclepias tuberosa rolfsii* all lend support to the hypothesis of "Orange Island" as a refugium of great antiquity, it has been known for an even longer time that the southeastern coastal plain has received many Appalachian fugitives from the rigors of Pleistocene glaciation[53] and Late Tertiary uplift.[54] Just how to distinguish the old settlers from the new frequently is indecisive.

The distribution of *A. lanceolata* (fig. 6) is not greatly unlike that of *A. tuberosa rolfsii* (fig. 5, upper left panel, which omits biometric evidence of *rolfsii-interior* hybrids westward along the Gulf coast to eastern Texas and of *rolfsii-tuberosa* hybrids up the Atlantic coast to Virginia[55]), and for the purposes of this discussion it is classified as Floridian. The species frequents brackish to fresh marshes, wet pine barrens, and low glades.

Interesting variants of the same basic pattern are found in *A. tomentosa* and *A. rubra* (fig. 6). In the former, which prefers pine barrens and sandy soil, a once continuous distribution has been broken into three meagre, widely disjunct populations. In the latter, a species of bogs, marshes, wet meadows, and low pine barrens, the once continuous range appears to be breaking into two even more widely separated segments to northeast and southwest, and has withdrawn entirely from Florida (if, in fact, it ever occurred there, which seems reasonable to assume).

But the distribution of *A. perennis* (fig. 6) is most disconcerting, since it combines such a "Floridian" range as we have been discussing with scattering stations up the Mississippi embayment to the Mississippi-Ohio lowlands, where it is evidently most congenially located of all. The distribution of *A. perennis* appears to be an advancing (or retreating?) arc from the Appalachians much as we have seen in *A. nuttalliana* (fig. 6) with respect to the Ozarks, and I am classifying it as Appalachian in consequence. The species inhabits low swampy ground, alluvial woods, sloughs, and ditches and is characteristically in the company of *Taxodium*. Because it is an extremely primitive species morphologically, and because its present distribution so clearly outlines the Late Cretaceous coast, I feel that it may well have frequented these cypress swamps for a corresponding period (admittedly, of course, because the present environment parallels to such an extent that of the past). The Oligocene Bembridge beds[56] have yielded the unmistakable comose

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[53] Kearney, T. H. The Lower Austral elements in the flora of the southern Appalachian region. Science n. s. 12:830. 1900.

[54] Braun, E. L. Some relationships of the flora of the Cumberland Plateau and Cumberland Mountains in Kentucky. Rhodora 39:193. 1937.

[55] Woodson, R. E., Jr. Ann. Missouri Bot. Gard. 34:353. 1947.

[56] Reid, E. M., and M. E. J. Chandler. The Bembridge Flora. London, 1926.

seeds of asclepiads, now far outside their native range, and I see no reason to accept that horizon as their first appearance.

Much less is known of the paleogeography of the western United States and Mexico than for the eastern United States, and analysis of plant distributions from that standpoint is scarcely justifiable in those areas. However, some possible information may be obtained by breaking down the data of Table I and interpreting them briefly in the light of comparative morphology and the broader details of historical geology.

Table II summarizes the incidence of the nine North American subgenera of *Asclepias* upon the six centers of concentration noted in fig. 4. From both tables it is strikingly apparent that the Mexican center includes more species than those of all the other five combined, and their diversification amongst the several subgenera is striking as well. Although no attempt has been made to generalize the maze of fig. 4 into sharply defined areas, it is obvious that in proportion to their relative sizes, the Mexican and the Floridian centers possess the most numerous and diversified species. The poorest in numbers and diversification is the Appalachian, if we exclude the Antillean from discussion at the moment.

Subgenus ASCLEPIAS, of course, is by far the richest of the genus, including over three-quarters of the total North American species. It is also diversified into eight indigenous series. Table III summarizes the distribution of species of the eight series amongst the six centers of concentration. Here, also, the Mexican and the Floridian centers are the richest in number and diversification of species, the Ozarkian mediocre, and the Appalachian and the Californian poorest, again excluding the Antillean.

TABLE II

NUMBERS OF SPECIES OF THE SUBGENERA OF *ASCLEPIAS* OCCURRING IN THE SIX CENTERS OF CONCENTRATION IN NORTH AMERICA

Subgenera	Centers of concentration					
	Appalachian	Ozarkian	Floridian	Mexican	Californian	Antillean
ASCLEPIAS	11	12	9	41	6	1
PODOSTEMMA				5	1	
ANANTHERIX			1			
ASCLEPIODELLA			2	4	1	
ACERATES	1	3	1	1		
SOLANOA				1	2	
POLYOTUS		1		2		
ASCLEPIODORA	1	1	1	6		
PODOSTIGMA			1	2		

As I have emphasized in previous paragraphs, I am not convinced that my subgenera and series of *Asclepias* are wholly natural, particularly the series. Nevertheless, this system of a neglected genus certainly is the most complete and objective available at present. And since a collateral consideration of phylogeny should be helpful to an understanding of geographical distribution, Table IV has been compiled as a final summary of the data of Table I. In it the relative affinities of the six centers of concentration are correlated with respect to the subgenera and series held in common.

TABLE III

NUMBER OF SPECIES OF SUBGENUS *ASCLEPIAS* OCCURRING IN THE SIX CENTERS OF CONCENTRATION IN NORTH AMERICA

Series	Centers of concentration					
	Appalachian	Ozarkian	Floridian	Mexican	Californian	Antillean
INCARNATAE	3	3	1	9	1	1
TUBEROSAE	2	2	2			
EXALTATAE	2	1		7		
GRANDIFLORAE				3		
SYRIACAE	2	4	2	5		
PURPURASCENTES	2	2	1	4		
MACROTIDES			1	7		
ROSEAE			2	6	5	

TABLE IV

AFFINITIES OF THE SIX CENTERS OF CONCENTRATION OF *ASCLEPIAS* IN NORTH AMERICA CORRELATED WITH RESPECT TO THE SUBGENERA AND SERIES HELD IN COMMON

Represented in all six centers		INCARNATAE
Represented in four centers: Appalachian, Ozarkian, Floridian, Mexican		SYRIACAE PURPURASCENTES ACERATES ASCLEPIODORA
Represented in 3 centers	Appalachian, Ozarkian, Floridian	TUBEROSAE
	Appalachian, Ozarkian, Mexican	EXALTATAE
	Floridian, Mexican, Californian	ROSEAE ASCLEPIODELLA
Represented in 2 centers	Ozarkian, Mexican	POLYOTUS
	Floridian, Mexican	MACROTIDES PODOSTIGMA
	Mexican, Californian	PODOSTEMMA SOLANOA
Represented in only 1 center	Floridian	ANANTHERIX
	Mexican	GRANDIFLORAE

It might have been anticipated that the affinities of the Appalachian center would be chiefly with the Ozarkian and only secondarily with the Floridian and the Mexican; that those of the Ozarkian should be primarily and about equally with the Appalachian and the Mexican, and only secondarily with the Floridian; and that the primary affinity of the Californian should be unquestionably with the Mexican. But it comes as more of a surprise that the primary affinities of the Floridian center should be about equally with the Mexican and the Ozarkian and only secondarily with the Appalachian, and that those of the Mexican, the most strongly pronounced of all, should be with the Floridian. Eight bicentric species of the Appalachians and the Ozarkian emphasize the close affinity of those centers. The three tricentric species of the Appalachian, the Ozarkian, and the Floridian are evidence of the distinctive character of the Floridian. No species center both in Mexico or California and any center to the east.

It will also be noticed from Table IV that the one major taxonomic group represented in all six centers, including the single species of the Antillean, is the most primitive series INCARNATAE, of the typical subgenus, and furthermore that the Appalachian and the Ozarkian centers, as a rule, have more primitive subgenera and series as well as tending to less endemism. The greatest degree of endemism is shared by the Mexican and the Floridian, and perhaps the Californian which appears as scarcely more than an annex of the Mexican.

The historical reconstruction that I make of these data is that the ancestral home of *Asclepias* in North America is in the Appalachian and the Ozark highlands, paleozoic land masses upon which the genus may well have been represented in some form as early as Cretaceous. The strong similarity and slight degree of differentiation of the asclepiad populations in those areas may be a reflection of their great age as well as the relative geologic and ecologic stability of their habitats. The rather slight differences between them may be due in large part to the Pleistocene ice sheets to the north, and to the south the intervening Mississippi embayment and later its alluvium to which few asclepiads have proven themselves adaptable.

The great diversification of *Asclepias* in the Floridian center may be due in part to the fluctuating "Orange Island" archipelago in early Tertiary, and partly to the southward migration to the Coastal Plain (as it became available) of certain Appalachian elements in late Tertiary and Pleistocene; it is difficult to distinguish them except by special methods. Of one thing we can be fairly certain: that the Antilles contributed nothing.

With the draining of the Cretaceous seas from the Rocky Mountain geosyncline, the western United States and Mexico gradually received asclepiad immigrants from the east: from the Ozarks and from Florida. The crest of this westward migration may have been approached in Pliocene. It is obvious that migration from the Ozarks could have taken place far earlier than from Florida. Lastly, the great diversification of the rich asclepiad flora of Mexico may be ascribed to adaptive radiation in response to the repeated Cenozoic orogenies culminating in Pleistocene. The Californian center, with its few species so slightly related to the Appalachian and the Ozarkian and so closely to the Mexican, may be considered the terminus of the westward migration.

A surprising thing about milkweeds is that they show so little of the ability to leap considerable distances, which one might expect to be the selective virtue of their comose seeds. An outstanding example of this anomaly is in the single species of the Greater Antilles, *A. nivea,* its failure to colonize the Bahamas or Florida, and conversely the absence of continental species on the islands. (The omnipresence of *A. curassavica* in the tropics of both hemispheres undoubtedly is due to escape from cultivation.) Such being the case, I would date the arrival of *Asclepias* in the Greater Antilles as Eocene, the time of their latest connection to the mainland of Central America. This would emphasize also the great speed with which the first asclepiads must have spread through Mexico and Central America as well as indicating their first source to have been the Ozarkian center, since Florida was archipelagic until Pliocene. It possibly is highly significant that the Antillean *A. nivea* is a species of the primitive series INCARNATAE and very closely related to the Mexican and Central American *A. angustifolia* and *A. woodsoniana.* That the speciation of *Asclepias* still continues in our time is emphasized dramatically by evidence of the recent birth of *A. tuberosa interior.*

Although the South American and the African centers of *Asclepias* are outside the scope of this study, I find it impossible to ignore them completely since, in some remote way, their history must be connected with that of the North American species. How does one account for the distantly trisected world distribution of the genus? To what extent may the phylogeny of the North American representation be tied up with that of the Southern Hemisphere?

There can be no shadow of doubt that the asclepiads of southeastern South America not only are congeneric with those of North America but are scarcely distinguishable from them. At one time I intended to include them within the present account but decided against doing so because the few species (and I cannot guess their number) show so little differentiation that the relatively few herbarium specimens available to me were insufficient for judging. All bear follicles on erect pedicels and the floral structure generally is similar to that of the North American INCARNATAE, but of size and coloration reminiscent of the TUBEROSAE. It would be most convenient, if a combined account were contemplated, to key them apart as a series solely on the basis of geography.

Probably none of the numerous African Asclepiadaceae would coincide wholly with my series of the typical subgenus ASCLEPIAS, and I anticipate that, if I were able to undertake a revision of the African species as a whole, an entirely different array of subgenera would emerge quite as diverse as those of North America, if not more so. In fact, I am fairly sure that I could not accommodate *Calotropis* within my system of *Asclepias,* extensible as it is, and the same would probably be true of *Schizoglossum* and others.

However, I am extremely suspicious of Bullock's[57] published intention of excluding *Asclepias* from Africa entirely, since I find it such a simple matter to include *A. fruticosa,* sporadically adventive in the New World, as representing merely a series of the typical subgenus ASCLEPIAS. The absence of attempts at generic keys in Bullock's preliminary notes also arouses misgivings which may be quieted by his final treatment for the 'Flora of East Africa.' Such keys, I anticipate, will bear a general resemblance to my keys to subgenera and series. Whatever our differences in matters of degree, I feel sure that Bullock and I would agree on the close alliance of the American and African Asclepiadeae.

Amongst the several possibilities of explaining the widely trisected distribution of *Asclepias* (in the broadest sense, to include those of Africa), only two commend themselves to me as worthy of serious consideration. One is trans-boreal migration, and the other is continental drift.

At the present day, no Asclepiadeae are indigenous to Eurasia save in the more xeric southeastern regions related to Africa. Nevertheless, comose seeds very suggestive of the tribe are figured by Reid and Chandler[58] in the Oligocene London clays, deposited under conditions probably more congenial to asclepiads than those now obtaining. Specifically, Pleistocene glaciation might be supposed capable of disrupting in most of Europe a primitive amphi-Atlantic distribution of ancestral *Asclepias,* which for our purpose must have extended at least intermittently from Patagonia northward to the Arctic in America and thence southward from boreal Europe to the Cape of Good Hope. The post-Pleistocene extreme xerism of northern Africa further might reduce the Eastern Hemisphere distribution of the genus essentially to what it is today.

It is in South America that this line of reasoning becomes excessively difficult, for here no indigenous Asclepiadeae are known, in fact from central Costa Rica to approximately the 16th parallel south, a distance of about 26 degrees of latitude. Admittedly, a vast majority of this area is tropical rain forest and not conducive to colonization by milkweeds of presently known preferences. On the other hand, I should imagine the savannas of the Roraima shield to be a likely habitat, as well certainly as extensive areas of the middle altitudes of the Andes. In fact, if the Cenozoic orogenies indeed were responsible for the rich diversification of *Asclepias* in Mexico, which seems an attractive hypothesis, it is difficult to see why the contemporary and closely related disturbances in the Andes could not have had a similar effect.

Finally, unless land connections in the Bering area could have been utilized for overland migration, which seems unlikely since we have seen reasons for assuming *Asclepias* to have reached the Pacific coast rather late in its development in North America, the obvious inability of modern species to cross even rather narrow straits in the Antilles would seem to militate against their chances of crossing the North

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[57] Bullock, A. A. Notes on African Asclepiadaceae, I. Kew Bull. 1952:426. 1952.

[58] Reid, E. M., and M. E. J. Chandler. The Bembridge Flora. London, 1926.

Atlantic, even utilizing Greenland, Iceland, and other way stations. Of course infinitely less would seem their ability of crossing the South Atlantic directly from Brazil to Africa or *vice versa.*

Although Wegener's hypothesis of Continental Drift is by no means generally accepted by geologists, it would provide by far the easiest solution for the occurrence of *Asclepias* in South America and in Africa. Following this line of reasoning, one might advance the theory that the contemporary centers of the genus in North America and in South America never were directly connected except by means of a by-pass through Africa. According to such a view, the geologic and ecologic stability of the southeastern United States and southeastern Brazil might explain the relative conservatism and striking similarity of the asclepiad flora in those regions.[59]

On the other hand, in Africa the drastic Cenozoic tectonic disturbances and vulcanism, particularly in East Africa, would introduce vast opportunities for adaptive radiation leading to the intricate biological diversification of today. Finally, the extreme xerism of North Africa might have obliterated representatives of the genus there in Post-Pleistocene. Of the two alternatives, I can see fewer *biological* objections to the Continental Drift.

ECONOMIC USES

Literature on the economic use of various species of *Asclepias* has become so voluminous since the outbreak of World War II that it is impossible to provide an adequate summary here. That function has been served very adequately by Miss Whiting[60] up to the year of publication. More recent literature may be sought amongst the entries in 'Biological Abstracts.'

Apparently utilization of *Asclepias* species was made by aborigines of both North America and Africa, chiefly with regard to the pericycle and phloem fibers of the stems and the seed coma (or "floss"). Pickering[61] recounts that the seed floss of *A. syriaca* was used as a stuffing for pillows and cushions by the colonists of New England, and that seeds of the plant were sent to England by Governor John Winthrop in 1670. Transmitted thence to the European Continent, *A. syriaca* soon became naturalized in southern France, Corsica, and Dalmatia. By the middle of the 19th century not only *A. syriaca* but also *A. incarnata* were in cultivation and freely escaping almost throughout Europe. Various attempts have been made in England, France, Germany, and Russia to bring the plant into full commercial use.

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[59] Without stronger evidence than comparative morphology (viz. polyploidy) it is quite impossible for me to conjecture whether *Asclepias* had its origin in the Northern Hemisphere or the Southern (cf. Camp, W. H. Distribution patterns in modern plants, etc. Ecol. Monogr. 17:159. 1947).

[60] Whiting, A. G. A summary of the literature on milkweeds (*Asclepias* spp.) and their utilization. U.S.D.A. Bibliogr. Bull. No. 2. 1943.

[61] Pickering, C. Chronological history of plants. p. 945. Boston, 1879.

The stem fibers of *Asclepias,* particularly of *A. incarnata* and *A. syriaca,* have been proposed as a substitute for flax and hemp, although generally inferior to them.[62] Milkweed latex has been mentioned repeatedly as a likely source of rubber in temperate latitudes. During World War II the seed floss proved to be the best substitute for kapok in the manufacture of life jackets for the U. S. Navy, and a harvest of 150,000 lbs. for that purpose was made during the year 1944.[63] Both the stem fiber and the floss have been advocated as stock for paper making. Secondary products of potential value include cellulose from the stems and a semi-drying oil from the seed. At the present time certain alkaloids of *Asclepias* are undergoing biochemical investigation, particularly with regard to the use of certain species as oral contraceptives.

During both World War I and World War II attention has turned to *Asclepias* as a widely diversified substitute for numerous strategically important plant products. Inevitably, after the close of hostilities and the resumption of normal commerce, the interest has died. The unfavorable showing of milkweed in peacetime is due essentially to the inability of a wild species to compete successfully with thoroughly domesticated and highly selected crop plants; what is truly surprising is that the comparison is not far more unfavorable. As a crop plant, a more serious handicap would be the more or less poisonous character of nearly all species, which makes *Asclepias* a dangerous pest in cattle and poultry areas.

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[62] Nelson, E. G., and S. T. Dexter. Fiber from the stems of common and swamp milkweed. Quart. Bull. Michigan Agr. Exp. Sta. 28:20. 1945.

[63] Gunning, H. A. Milkweed floss for the Navy. U.S.D.A. Soil Conserv. 9:195. 1944.

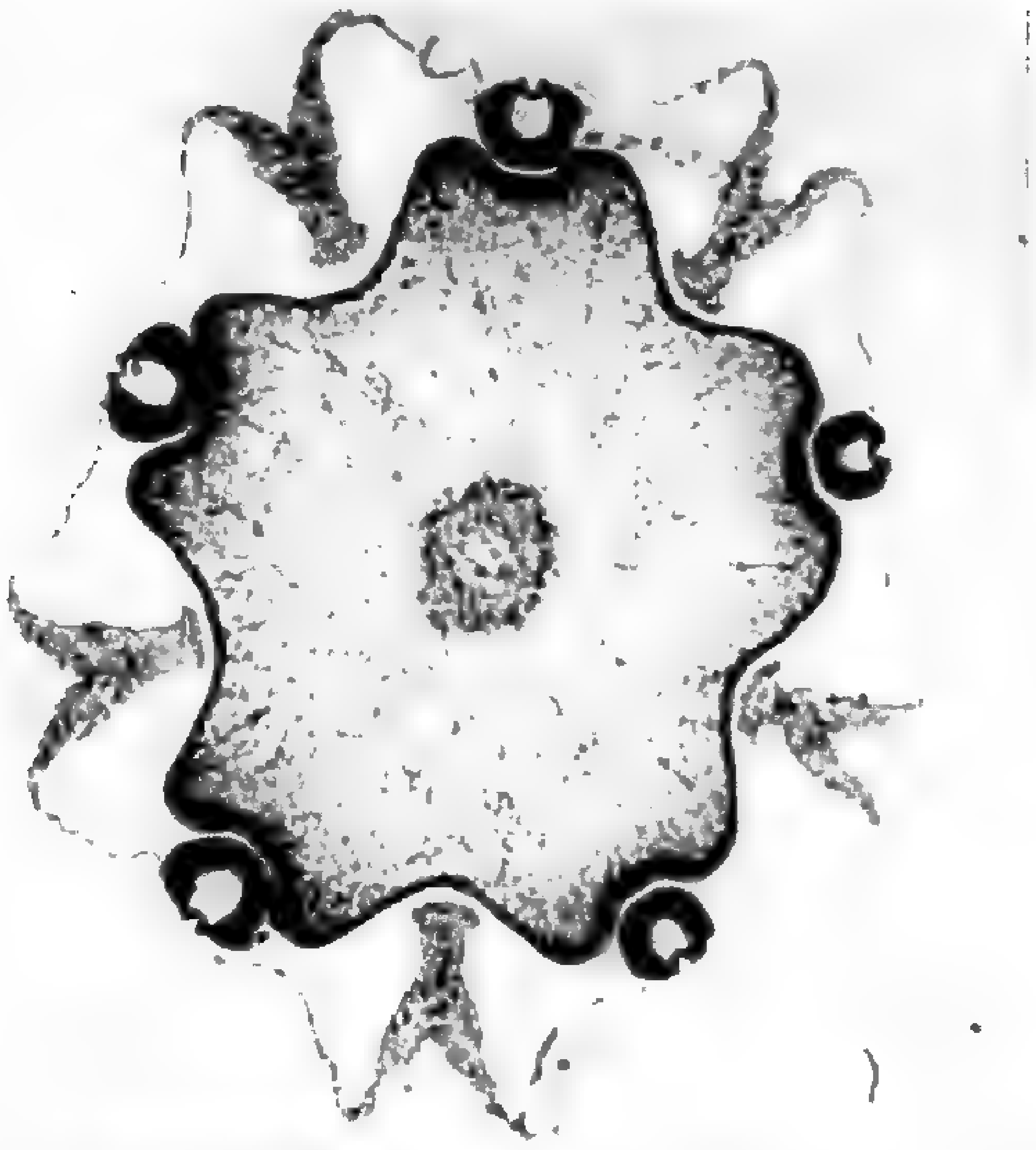
EXPLANATION OF PLATE

PLATE 1

Wasp visiting *Asclepias syriaca.* Inset: multiple pollinia on claw of bee (×7).

Portrait by Claude E. Johnston.

WOODSON — ASCLEPIAS



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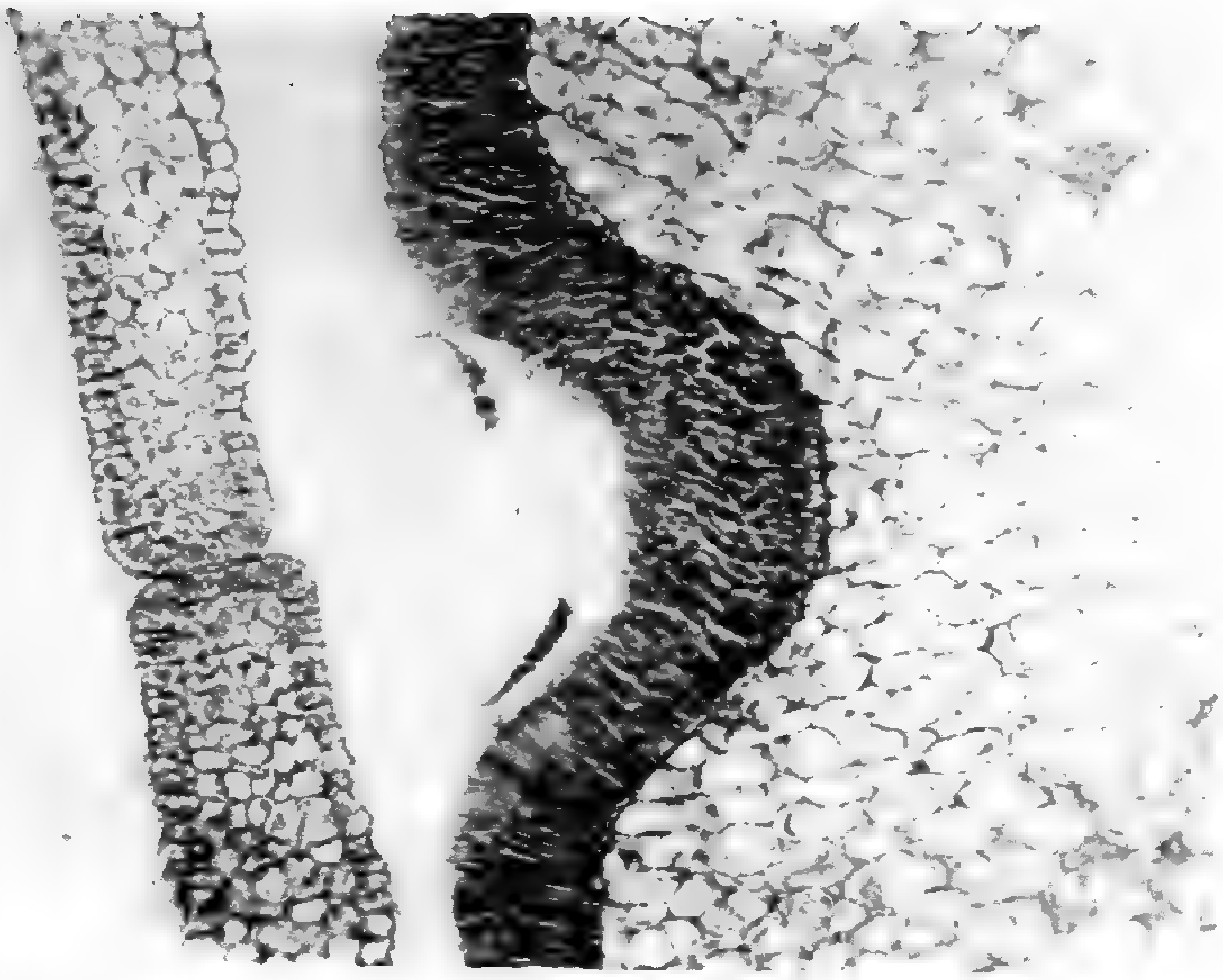

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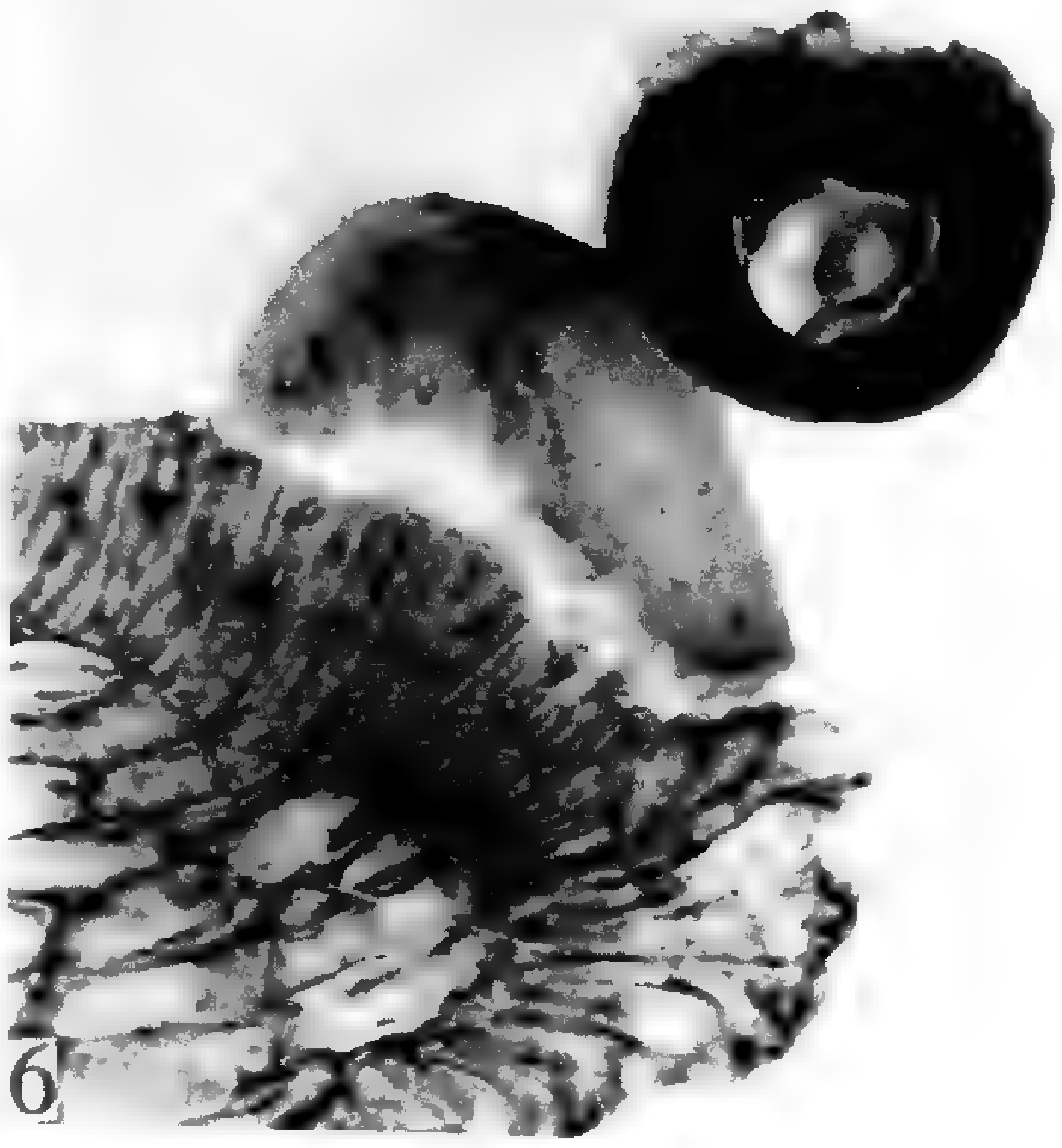

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WOODSON — ASCLEPIAS

EXPLANATION OF PLATE

PLATE 2

Asclepias curassavica

Fig. 1. Transverse section of stigma head, showing furrows within which translator glands are secreted (× 19).

Fig. 2. Stigma furrow, showing first secretions of translator gland (× 110).

Fig. 3. Secretions of translator gland: later stage (× 110).

Fig. 4. Translator gland fully formed: photographed with red filter to show striated structure (× 110).

Fig. 5. Attachment of translator arms to gland: green filter (× 110).

Fig. 6. Attachment of translator arm to pollinium sac: green filter (× 110).

Explanation of Plate

PLATE 3

Asclepias curassavica

Fig. 1. Transverse section of anther head, showing five concrescent anthers (with pollinium sacs) and intervening stigmatic chambers (× 19).

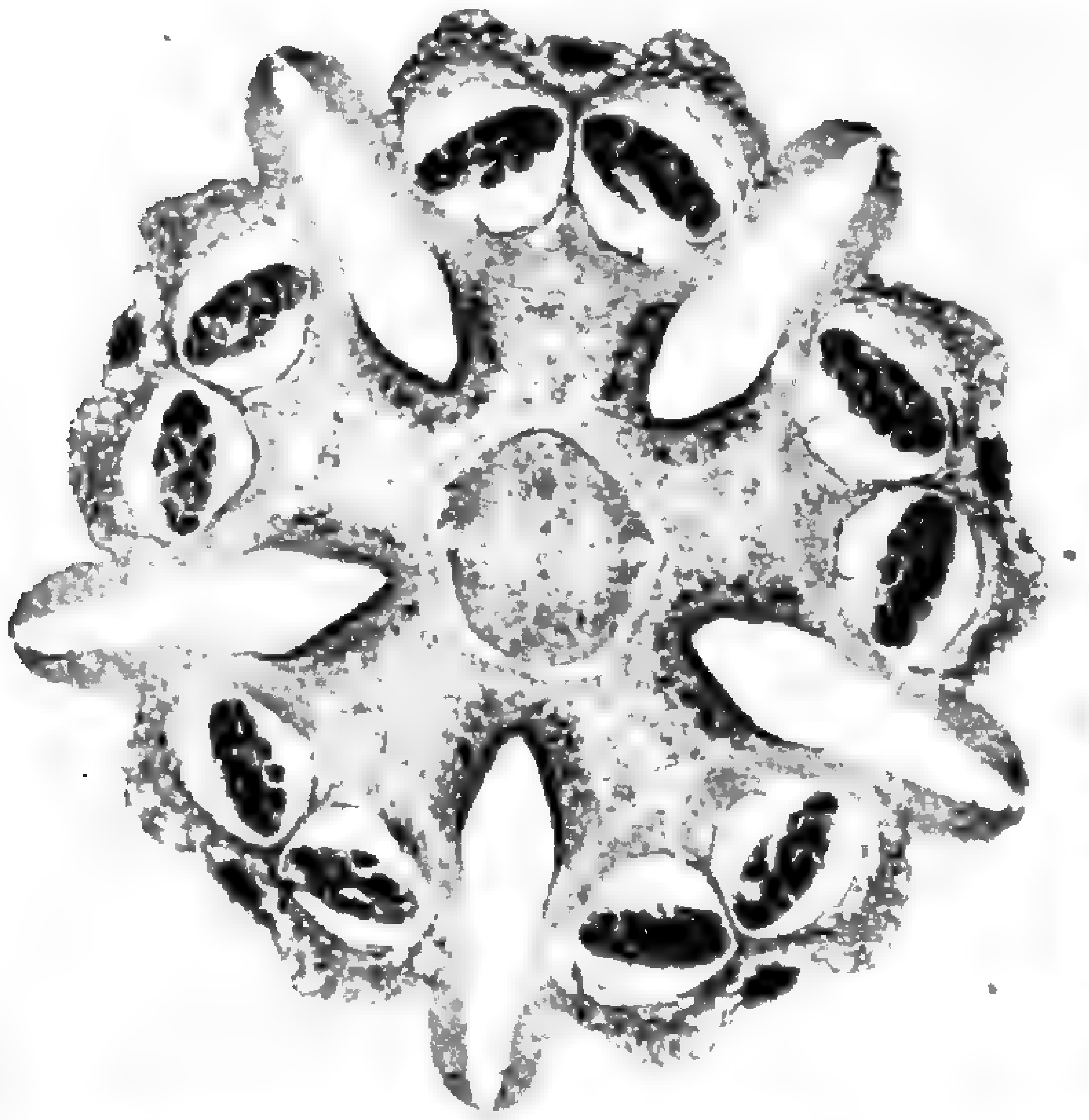
Fig. 2. Pollen mother cells surrounded by unequal tapetum: red filter (× 110).

Fig. 3. Pollen diads: red filter (× 110).

Fig. 4. Pollen tetrads, with suberization of intervening walls and disorganization of tapetum: red filter (× 110).

Fig. 5. Mature pollinium sac: red filter (× 110).

Fig. 6. Pollen mother cells surrounded by unequal tapetum: green filter to show lipoid bodies in outer tapetum (× 110).



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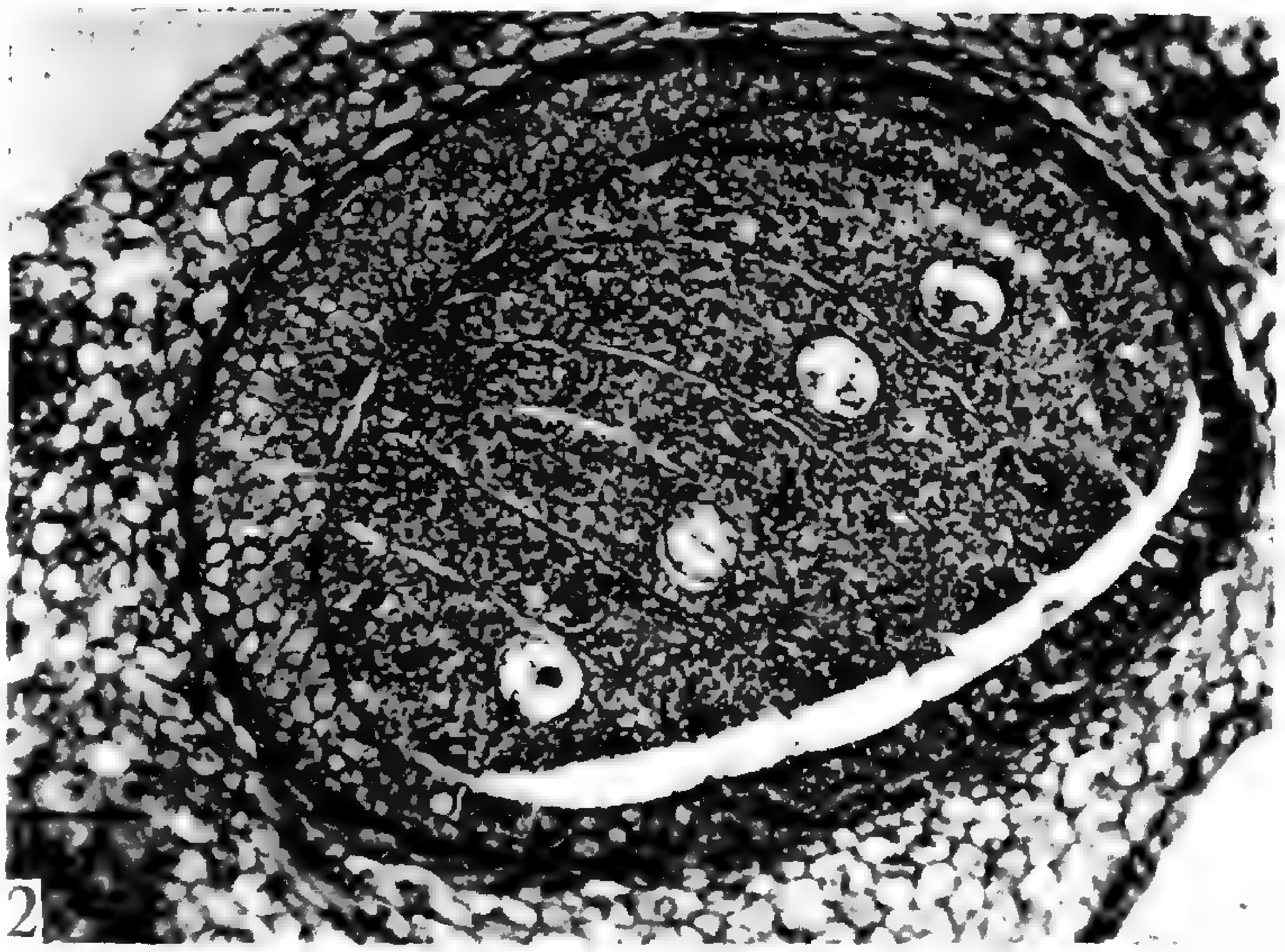

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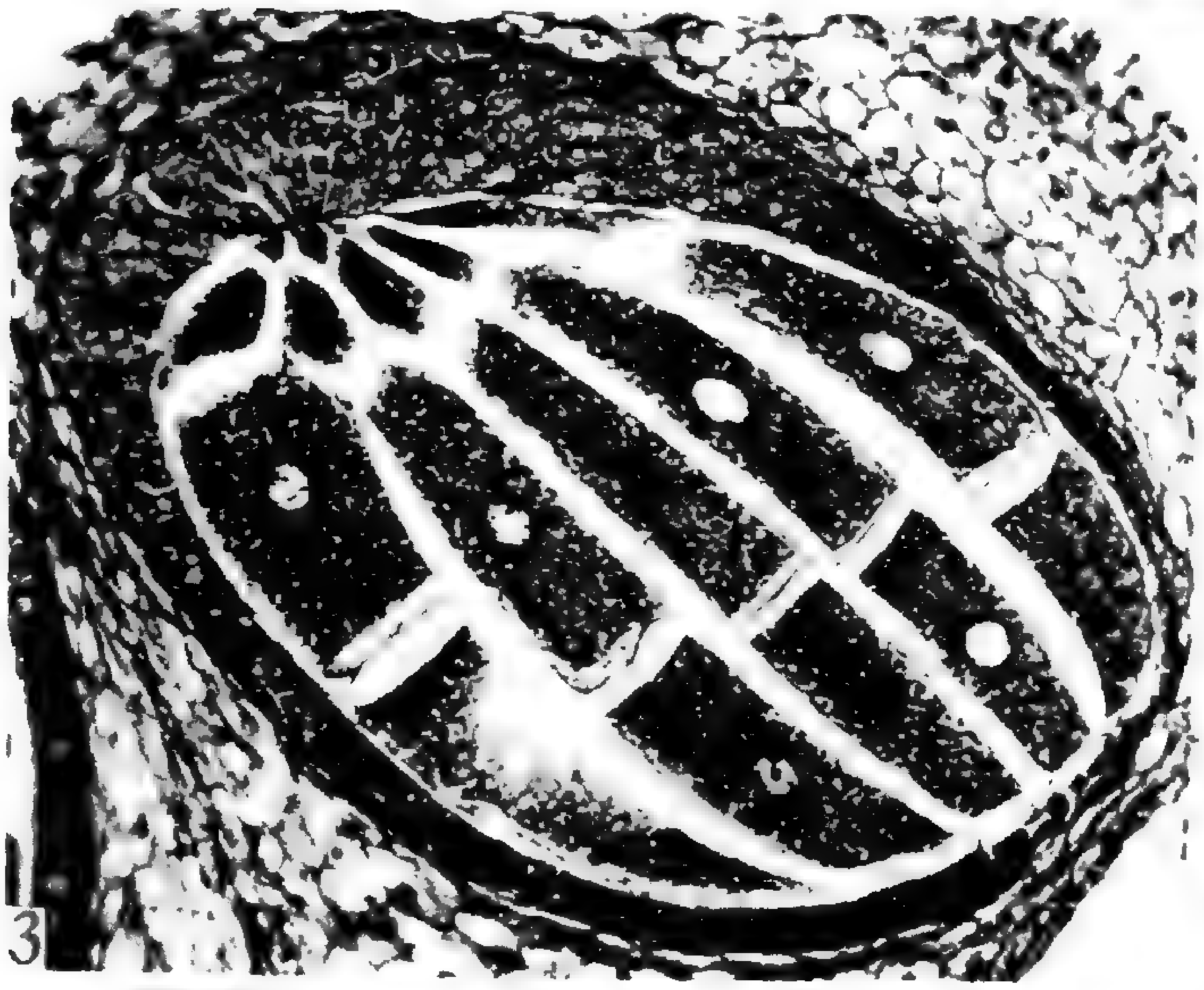

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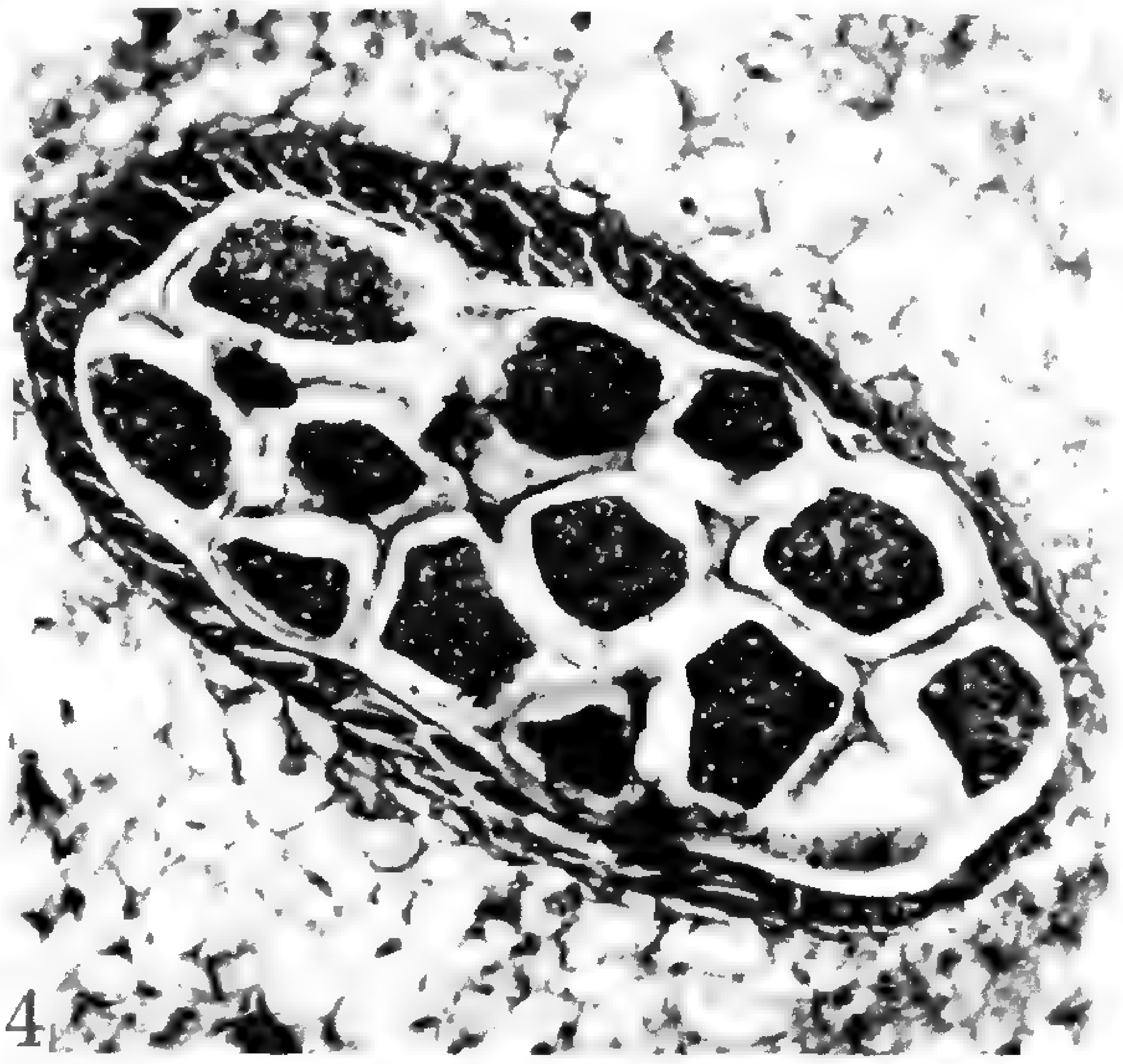

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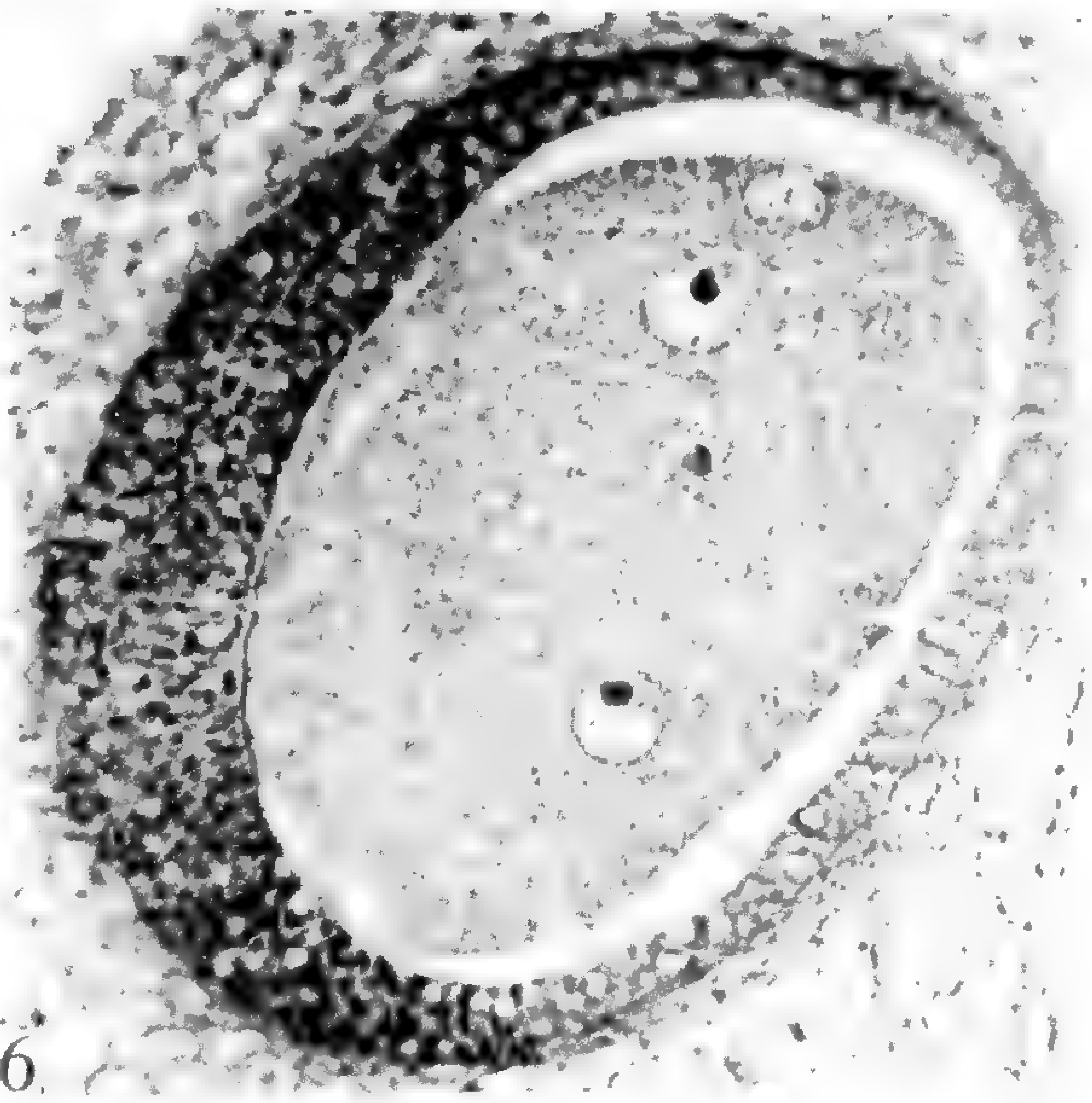

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WOODSON — ASCLEPIAS

TAXONOMY

ASCLEPIAS L. Sp. Pl. 214. 1753. [T.: *A. syriaca* L.]

Gomphocarpus R. Br. in Mem. Wern. Soc. 1:37. 1809. [T.: *G. arborescens* (L.) R. Br,]
Acerates Ell. Sketch Bot. South Car. 1:316. 1817. [T.: *A. longifolia* (Michx.) Ell.]
Podostigma Ell. *loc. cit.* 326. 1817. [T.: *P. pubescens* Ell.]
Anthanotis Raf. Fl. Ludov. 52, 149. 1817. [T.: *A. procumbens* Raf.]
Anantherix Nutt. Gen. North Am. Pl. 1:169. 1818; A. Gray, in Proc. Amer. Acad. 12:66. 1877. [T.: *A. connivens* (Baldw.) A. Gray]
Stylandra Nutt. *loc. cit.* 170. 1818. [T.: *S. pumila* Nutt.]
Otaria HBK. Nov. Gen. 3:192. 1819, nom. prov.; ex G. Don, Gen. Hist. 4:144. 1838. [T.: O. *auriculata* (HBK.) G. Don]
Acerotis Raf. New Fl. North Amer. 1:49. 1836. [Based on *Acerates* Ell.]
Oligoron Raf. *loc. cit.* 60. 1836. [T.: *O. longifolium* (Michx.) Raf.]
Otanema Raf. *loc. cit.* 61. 1836. [T.: *O. latifolia* Raf.]
Polyotus Nutt. in Trans. Am. Phil. Soc. n. s. 5:199. 1837. [T.: *P. angustifolius* Nutt,]
Asclepiodora A. Gray, in Proc. Amer. Acad. 12:66. 1877. [T.: *A. viridis* (Walt.) A. Gray]
Schizonotus A. Gray, *loc. cit.* 1877, non Lindl. (1840). [T.: *S. purpurascens* (A. Gray) A. Gray]
Solanoa Greene, Pittonia 2:67. 1890. [Based on *Schizonotus* A. Gray]
Solanoana O. Ktze. Rev. Gen. 2:421. 1891. [Based on *Solanoa* Greene]
Oxypteryx Greene, Pittonia 3:234. 1897. [T.: *O. arenicola* (Nash) Greene]
Podostemma Greene, loc. cit. 235. 1897. [T.: *P. longicornu* (Benth.) Greene]
Biventraria Small, Man. Fl. Southeast. U. S. 1072. 1933. [T.: *B. variegata* (L.) Small]
Asclepiodella Small, loc. cit. 1073. 1933. [T.: *A. feayi* (Chapm.) Small]

Calyx lobes 5, equal, divided nearly to the receptacle, bearing few to many minute glandular squamellae within at the base. Corolla rotate, the lobes 5, valvate, equal, reflexed, spreading or rarely erect. Gynostegium definitely stipitate to subsessile; corona of 5 hoods attached to the column and subtending the connivent anthers, the hoods cucullate to clavate with various modifications, more or less stipitate to sessile and deeply saccate at the basal attachment to the column, usually bearing an internal horn or crest; anthers 2-locular, with more or less prominent corneous marginal wings enclosing the 5 stigmatic chambers and with membranaceous apical appendages, the pollinia paired and pendulous from the translator arms, flat and uniformly fertile, enclosing granular pollen with thin hyaline intine; stigma head peltate, more or less 5-gonal. Fruit follicular, containing many compressed comose or rarely naked seeds. Herbs, rarely fruticose or suffruticose, perennial or rarely annual, usually laticiferous. Leaves usually decussate, infrequently whorled or irregularly approximate. Inflorescence terminal or interpetiolar, umbelliformly cymose, very rarely *(A. sperryi)* reduced to a solitary flower.

KEY TO THE SUBGENERA

A. Hoods more or less stipitate or substipitate, the basal attachment not deeply saccate.
  B. Hoods cucullate, the base involute or conduplicate but wholly laminate, the adnate horn (rarely absent) evident to the column or nearly so...I. ASCLEPIAS (p. 48)
  BB. Hoods spatulate to clavate, with a conspicuous solid stipe and only the margins free to the base, the adnate horn merging with the basal stipe.
    C. Hoods spatulate, broadly laminate above the middle; translator arms much shorter than the pollinium sacs ....II. PODOSTEMMA (p. 152)

CC. Hoods clavate, scarcely laminate; translator arms about three times as long as the pollinium sacs .... III. ANANTHERIX (p. 160)

AA. Hoods very sessile, the basal attachment deeply saccate, the adnate horn (frequently absent) typically reduced to an inconspicuous and isolated crest or terminal appendage.
  B. Hoods not deflexed from the anther head.
    C. Hoods without external basal appendages or merely somewhat keeled laterally.
      D. Hoods freely open above, the horn or crest present (except in *A. cordifolia*) .... IV. ASCLEPIODELLA (p. 161)
      DD. Hoods with the orifice appressed to the anthers, the horn absent .... V. ACERATES (p. 169)
      DDD. Hoods wholly or mostly closed by the closely involute margins, typically deeply bifid dorsally, the horn absent or reduced to an isolated incurved appendage.... VI. SOLANOA (p. 176)
    CC Hoods with 2 conspicuous external laminate basal appendages .... VII. POLYOTUS (p. 181)
  BB. Hoods sharply deflexed from the anther head (only slightly so in *A. elata*), thence typically with ascending involute, conduplicate, or clavate tips.
    C. Anther head sessile and immediately subtended by the hoods .... VIII. ASCLEPIODORA (p. 185)
    CC. Anther head borne on a stipe together with the alternating lobules high above the hoods .... IX. PODOSTIGMA (p. 196)

SUBGENUS I. ASCLEPIAS

KEY TO THE SERIES

a. Anther head about as long as broad, or slightly longer or slightly shorter; column cylindric or conic, rarely obconic; horns usually gradually tapered and arching over the anther head.
  b. Hoods broadly rounded or flattened dorsally.
    c. Hoods without sharply incised marginal auricles (except in *A. verticillata*); leaves opposite, verticillate, or spirally approximate; follicles erect on erect pedicels (pendulous or subpendulous in *A. perennis* and *A. leptopus*) .... Series 1. INCARNATAE (p. 49)
    cc. Hoods with sharply incised marginal auricles; leaves opposite (except in *A. tuberosa*); follicles erect on deflexed pedicels.
      d. Hoods two to three times as long as the anther head, the marginal auricles basal and inflexed .... Series 2. TUBEROSAE (p. 74)
      dd. Hoods slightly shorter than the anther head to about half longer, the marginal auricles incised toward the tip, usually spreading .... Series 3. EXALTATAE (p. 82)
  bb. Hoods strongly conduplicate, sharply keeled dorsally, with very broadly incised marginal auricles; follicles erect on deflexed pedicels .... Series 4. GRANDIFLORAE (p. 95)

aa. Anther head about three-quarters as long as broad or somewhat shorter; column broadly obconic to essentially obsolete; horns usually abruptly beaked and sharply inflexed toward or over the anther head, occasionally absent.
  b. Hoods gradually rounded to acuminate; horns adnate to about midway of the hood or below when present.
    c. Hoods with sharply incised marginal auricles, usually broadly rounded dorsally; follicles erect on deflexed pedicels (erect on erect pedicels in *A. quadrifolia* and *A. viridula*; pendulous in *A. humilis* and *A. pellucida*) .... Series 5. SYRIACAE (p. 99)
    cc. Hoods without sharply incised marginal auricles, but usually with broader lobing.
      d. Hoods usually broadly flattened dorsally, usually abruptly constricted to a short basal stipe; follicles erect on deflexed pedicels .... Series 6. PURPURASCENTES (p. 114)
      dd. Hoods narrowly keeled dorsally, sessile or subsessile; follicles erect on deflexed pedicels (erect on erect pedicels in *A. michauxii*) .... Series 7. MACROTIDES (p. 127)

bb. Hoods truncate or very abruptly rounded at the tip, keeled dorsally; horns usually adnate the length of the hood or nearly so when present.

c. Horns present; follicles erect on deflexed pedicels (pendulous or subpendulous in *A. labriformis*) .... Series 8. ROSEAE (p. 135)

cc. Horns absent or reduced to glandular crests; follicles erect on deflexed pedicels. African species sporadically introduced in the American tropics............ Series 9. FRUTICOSAE (p. 151)

Series 1. INCARNATAE

KEY TO THE SPECIES

a. Hoods slightly shorter to about half longer than the anther head; translator arms ligular, narrower than the gland.

b. Leaves opposite.

c. Hoods slightly shorter to very slightly longer than the anther head.

d. Inflorescences usually paired at the upper nodes, solitary below; flowers bright pink (rarely white); leaves broadly oblong-elliptic to narrowly oblong-lanceolate. Southern Nova Scotia, Quebec, Ontario, and Manitoba; Maine to Florida and westward to Utah and New Mexico .... 1. *A. incarnata*

dd. Inflorescences solitary at the upper nodes; flowers white, the corolla occasionally tinged with purple without.

e. Leaves oval to narrowly elliptic.

f. Follicles erect on erect pedicels; seeds comose. Southwestern Texas; Coahuila and Nuevo León .... 2. *A. texana*

ff. Follicles pendulous; seeds naked. South Carolina to Florida and westward to eastern Texas, lower Mississippi Valley to southern Indiana, Illinois and Missouri .... 3. *A. perennis*

ee. Leaves narrowly lanceolate to linear-lanceolate, the base more or less hastate. Vera Cruz to Oaxaca and Chiapas; Guatemala; Honduras; El Salvador; Nicaragua; Costa Rica; Colombia (?) .... 4. *A. woodsoniana*

eee. Leaves linear, attenuate at the base.

f. Inflorescences lateral at several upper nodes, rather few-flowered and lax; flowers greenish white. South-central Texas .... 5. *A. linearis*

ff. Inflorescences terminal or lateral at few upper nodes, many-flowered and dense; flowers strongly suffused with purple. Tamaulipas and San Luis Potosí .... 6. *A. pseudorubricaulis*

cc. Hoods one-third to half longer than the anther head.

d. Column somewhat longer than broad; flowers about 1.2–1.5 cm. long from hood- to corolla lobe-tip, the corolla bright red (rarely white or yellow). Throughout tropical and subtropical America .... 7. *A. curassavica*

dd. Column about as long as broad or somewhat shorter; flowers about 1 cm. long from hood- to corolla lobe-tip or somewhat shorter, white or pink, sometimes slightly suffused with purple without.

e. Leaves ovate- to lanceolate-elliptic, conspicuously petiolate, more or less pubescent beneath. Antilles .... 8. *A. nivea*

ee. Leaves linear to linear-lanceolate, inconspicuously petiolate, glabrous to inconspicuously pilosulose beneath. Southern Arizona; Tamaulipas to Sonora and southward to Chiapas .... 9. *A. angustifolia*

bb. Leaves verticillate or spirally approximate.

c. Leaves verticillate.

d. Leaves more or less heterophyllous at the nodes, rather lax and spreading; stems usually with dwarf vegetative branches bearing reduced opposite leaves; hoods slightly shorter than the anther head.

e. Inflorescences paired or clustered at the upper nodes; flowers grayish pink to white; leaves oblong- to linear-lanceolate. Idaho and Utah to Washington, Oregon, and California; Baja California .... 10. *A. fascicularis*

ee. Inflorescences usually solitary at the upper nodes; flowers white; leaves linear. Colorado to Texas and westward to Idaho, Utah, and Arizona; San Luis Potosí to Sonora .... 11. *A. subverticillata*

dd. Leaves isophyllous at the nodes, rather strictly ascending; stems usually without dwarf vegetative branches or those with verticillate leaves.

e. Leaves elliptic to narrowly elliptic-lanceolate; inflorescences clustered or paired at the upper nodes; flowers greenish white and more or less suffused with purple; hoods slightly longer than the anther head, without incised marginal auricles. Nuevo Leon southward to Oaxaca ....12. *A. mexicana*

ee. Leaves filiform; inflorescences solitary or paired at the upper nodes; flowers greenish white; hoods slightly shorter than the anther head and usually with incised marginal auricles. Southern Ontario and Manitoba; Massachusetts to Florida and westward to North Dakota and Texas........13. *A. verticillata*

cc. Leaves spirally approximate or the lowest occasionally verticillate, filiform; hoods slightly longer than the anther head and without incised marginal auricles. North Dakota to Texas and westward to Wyoming and New Mexico........14. *A. pumila*

aa. Hoods about two to three times as long as the anther head; translator arms broadly triangular, larger than the gland.

b. Plants suffruticose; leaves caducous, filiform; flowers relatively small, greenish white; horns adnate to about midway of the hoods. Chihuahua, Sonora, and Sinaloa....15. *A. leptopus*

bb. Plants herbaceous; leaves persistent, linear to linear-lanceolate; flowers moderately large, the corolla bright red to pinkish, the hoods yellow; horns adnate to near the tip of the hoods. Chihuahua to Sinaloa and Nayarit ....16. *A. gentryi*

1. Asclepias incarnata L. Sp. Pl. 215. 1753. [T.: Linn. Herb. London, no. *310.25*, photo!]

Herbaceous perennials from rather short and superficial root-stalks. Stems usually fairly stout, 4–15 dm. tall, simple to copiously branched. Leaves opposite

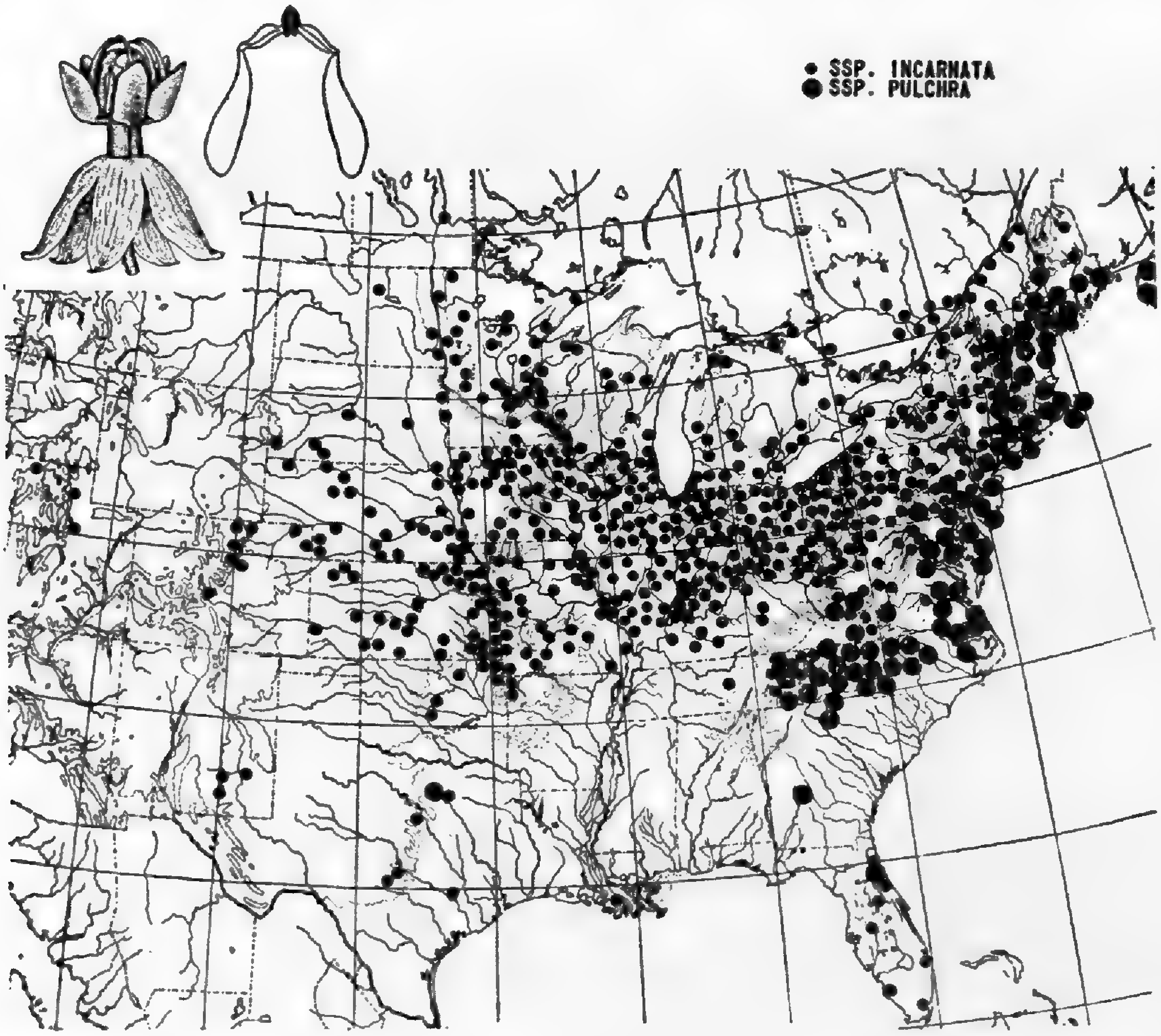

Fig. 7. *Asclepias incarnata* L.*

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* In all figures: flowers × 2½, pollinia × 10.

or very rarely certain nodes condensed to form a false whorl, petiolate, ovate-elliptic to linear-lanceolate, the apex acute to acuminate, the base obtuse to somewhat cordate, 5–15 cm. long, 0.5–4.0 cm. broad, membranaceous; petioles 0.4–1.0 cm. long. Inflorescences usually paired at the upper nodes, solitary below, several- to many-flowered; peduncles 1.5–7.0 cm. long; pedicels 1.0–1.5 cm. long. Flowers rather small; calyx lobes linear-oblong, 1.0–1.5 mm. long, pilosulose; corolla bright pink or rarely white, reflexed-rotate, the lobes 3–4 mm. long; gynostegium paler pink or rarely white, the column cylindric, 1.0–1.5 mm. long, about 1 mm. wide, the hoods cucullate, rounded at the tip, about 1.5 mm. long, the internal horn narrowly acicular, slightly incurved over the stigma head, somewhat longer than the hood; anther head about 1.5 mm. long. Follicles erect on erect pedicels, fusiform, long-attenuate, 7–9 cm. long, 0.8–1.2 cm. thick, smooth, glabrous to generally pilosulose; seeds broadly oval, 7–10 mm. long, the white coma about 2 cm. long.

KEY TO THE SUBSPECIES

Plants scatteringly and inconspicuously pubescent to essentially glabrous; stems usually repeatedly branching; leaves usually rather narrowly oblong- to linear-lanceolate, the apex gradually acuminate, the base obtuse to truncate, rather long-petiolate; Southern Quebec, Ontario, and Manitoba; Maine to Florida and westward to Utah and New Mexico.. 1a. *A. incarnata incarnata*

Plants generally and conspicuously pubescent; stems simple or branching infrequently; leaves ovate- to broadly oblong-elliptic, the apex acute to abruptly acuminate, the base rounded or somewhat cordate, infrequently broadly obtuse, rather short-petiolate. Nova Scotia; Maine to South Carolina, adventive in Ohio, Florida, and Texas................1b. *A. incarnata pulchra*

1a. ASCLEPIAS INCARNATA ssp. INCARNATA

Asclepias verecunda Salisb. Prodr. 150. 1796, nom. nud.
Asclepias amoena Brongn. in Ann. Sci. Nat. Ser. I, 24:275, *t. 13*. 1831, non L., ex ic.
Asclepias albiflora Raf. New Fl. N. Amer. 4:62. 1836, ex char.
Asclepias incarnata var. *longifolia* A. Gray, in Proc. Amer. Acad. 12:67. 1877, nom nud.
Asclepias incarnata f. *albiflora* Heller, in Bull. Torrey Bot. Club 21:24. 1894, ex char.

Watersides and moist soil. Southern Quebec, Ontario, and Manitoba; Maine to Florida and westward to Utah and New Mexico. Flowering from May to September.

CANADA: MANITOBA: St. Clement County. ONTARIO: Bruce, Carleton, Elgin, Essex, Hastings, Huron, Kenora, Lanark, Manitoulin Island, Middlesex, Nipissing, Northumberland, Parry Sound, Peel, Victoria, Welland, and Wellington counties. QUEBEC: Bellechasse, Brome, Chambly, Hochelaga, Hull, Labelle, Lotbiniere, Montmagny, Nicolet, and Pontiac counties.

UNITED STATES:

ARKANSAS: Benton and Washington counties.

COLORADO: Boulder, Denver, Fremont, Jefferson, Larimer, Logan, Weld, and Yuma counties.

CONNECTICUT: Litchfield and Middlesex counties.

FLORIDA: Collier, Dade, DeSoto, Duval, Flagler, Lake, Palm Beach, Polk, and Volusia counties.

ILLINOIS: Adams, Cass, Champaign, Clay, Clinton, Coles, Cook, Crawford, DeKalb, DuPage, Douglas, Effingham, Fayette, Iroquois, Jackson, Jefferson, Lake, LaSalle, Lee, Livingston, Logan, McHenry, McLean, Macon, Mason, Monroe, Ogle, Peoria, Piatt, Pike, Richland, Rock Island, St. Clair, Saline, Stephenson, Stark, Tazewell, Vermilion, Wabash, Wayne, Whiteside, and Woodford counties.

INDIANA: Allen, Blackford, Boone, Carroll, Cass, Clay, Clinton, Dearborn, DeKalb, Dubois, Elkhart, Fayette, Franklin, Fulton, Gibson, Grant, Greene, Hancock, Harrison, Huntington, Jackson, Jay, Jefferson, Jennings, Knox, Kosciusko, LaGrange, Lake, LaPorte, Marshall, Miami, Montgomery, Newton, Noble, Orange, Owen, Parke, Pike, Porter, Posey, Randolph, St. Joseph, Scott, Shelby, Spencer, Starke, Steuben, Sullivan, Tippecanoe, Tipton, Vanderburgh, Wabash, Warren, Warrick, Wayne, Wells, White, and Whitley counties.

IOWA: Allamakee, Benton, Black Hawk, Boone, Calhoun, Cerro Gordo, Chickasaw, Clay, Clayton, Clinton, Dallas, Decatur, Dickinson, Emmet, Fayette, Floyd, Hamilton, Hancock, Humboldt, Jasper, Johnson, Kossuth, Lee, Linn, Lucas, Monona, Muscatine, O'Brien, Pocahontas, Palo Alto, Polk, Poweshiek, Ringgold, Sac, Sioux, Story, Tama, Union, Van Buren, Wright, Woodbury, Warren, Webster, Winnebago, and Winneshiek counties.

KANSAS: Bourbon, Brown, Cherokee, Cloud, Crawford, Decatur, Doniphan, Douglas, Ellsworth, Graham, Hamilton, Harper, Harvey, Hodgeman, Jackson, Johnson, Kingman, Kiowa, Labette, Leavenworth, Linn, Marshall, Miami, Neosho, Osage, Pottawatomie, Pratt, Reno, Republic, Rice, Riley, Rooks, Saline, Sedgwick, Sheridan, Shawnee, Stafford, Sumner, Washington, and Woodson counties.

KENTUCKY: Carroll, Fayette, Hart, Jessamine, Taylor, Union, Warren, Washington, and Wayne counties.

LOUISIANA: Terrebonne Parish.

MAINE: Androscoggin, Aroostook, Kennebec, Penobscot, Sagadahoc, and Somerset counties.

MASSACHUSETTS: Berkshire County.

MICHIGAN: Barry, Berrien, Calhoun, Cheboygan, Emmet, Gratiot, Ingham, Kalamazoo, Kent, Macomb, Newaygo, Oakland, Shiawassee, Van Buren, and Washtenaw counties.

MINNESOTA: Anoka, Becker, Brown, Carlton, Carver, Cass, Chisago, Clay, Clearwater, Cook, Douglas, Faribault, Goodhue, Hennepin, Houston, Hubbard, Itaska, Kandiyohi, Kanabec, Otter Tail, Polk, Pope, Ramsey, Red Wood, Roseau, St. Louis, Stearns, Wabasha, Waseca, Washington, Winona, and Wright counties.

MISSOURI: Barton, Bates, Boone, Butler, Clay, Dallas, DeKalb, Dent, Greene, Grundy, Henry, Howell, Jackson, Jasper, Jefferson, McDonald, Macon, Marion, Pettis, Phelps, Pike, Ralls, St. Louis, Scott, Stone, Texas, and Webster counties.

NEBRASKA: Brown, Cass, Chase, Cherry, Custer, Dawson, Dixon, Dodge, Douglas, Dundy, Franklin, Gage, Hooker, Kearney, Lincoln, Lancaster, Merrick, Otoe, Polk, Sarpy, Saunders, Sheridan, Thomas, and Webster counties.

NEW HAMPSHIRE: Cheshire, Coos, and Grafton counties.

NEW JERSEY: Middlesex, Somerset, and Warren counties.

NEW MEXICO: Chaves, Lincoln, and Otero counties.

NEW YORK: Cattaraugas, Cayuga, Chautauqua, Chenango, Clinton, Cortland, Delaware, Dutchess, Essex, Franklin, Greene, Herkimer, Jefferson, Lewis, Livingston, Madison, Niagara, Oneida, Onondaga, Orange, Oswego, Otsego, St. Lawrence, Saratoga, Seneca, Schenectady, Sullivan, Tompkins, Ulster, Washington, and Warren counties.

NORTH DAKOTA: Benson, Cass, and Richland counties.

OHIO: Ashtabula, Athens, Auglaize, Belmont, Brown, Butler, Carroll, Champaign, Clark, Clermont, Columbiana, Coshocton, Cuyahoga, Darke, Delaware, Erie, Fayette, Fairfield, Franklin, Gallia, Geauga, Guernsey, Hamilton, Harrison, Hardin, Highland, Hocking, Holmes, Huron, Jackson, Jefferson, Knox, Lake, Licking, Logan, Lorain, Madison, Mercer, Miami, Montgomery, Muskingum, Noble, Ottawa, Perry, Pike, Preble, Richland, Ross, Shelby, Scioto, Stark, Summit, Tuscarawas, Union, Warren, Washington, Wayne, Wood, and Wyandot counties.

OKLAHOMA: Cleveland, Craig, Delaware, Oklahoma, Osage, and Ottawa counties.

PENNSYLVANIA: Allegheny, Armstrong, Beaver, Bedford, Blair, Butler, Cambria, Chester, Clarion, Clearfield, Crawford, Erie, Fayette, Greene, Huntingdon, Indiana, Jefferson, Juniata, Lackawanna, Lancaster, Lawrence, Leigh, McKean, Mercer, Monroe, Montgomery, Montour, Northampton, Perry, Philadelphia, Somerset, Snyder, Venango, Warren, Washington, Wayne, and Westmoreland counties.

SOUTH DAKOTA: Bennett, Brookings, Clay, Custer, Deuel, Spink, Stanley, and Washington counties.

TENNESSEE: Blount, Cumberland, Grainger, Hawkins, Jefferson, Knox, Monroe, Rutherford, and Sullivan counties.

TEXAS: Dallas, Gonzales, Gillespie, Hood, and Kerr counties.

UTAH: Box Elder, Davis, and Utah counties.

VERMONT: Addison, Bennington, Caledonia, Chittenden, Essex, Franklin, Orleans, Rutland, and Windsor counties.

VIRGINIA: Arlington, Bath, Craig, Giles, Montgomery, Prince George, Rockingham, Shenandoah, Surry, and Warren counties.

WEST VIRGINIA: Barbour, Berkeley, Cabell, Grant, Hampshire, Hardy, Harrison, Jackson, Marion, Mason, Mercer, Mineral, Monongalia, Ohio, Preston, Putnam, Raleigh, Randolph, Ritchie, Summers, Upshur, Wetzel, and Wirt counties.

WISCONSIN: Ashland, Bayfield, Buffalo, Burnett, Columbia, Crawford, Dane, Grant, Iowa, Jefferson, Kenosha, Langlade, Lincoln, Marathon, Marinette, Marquette, Milwaukee, Ozaukee, Polk, Rock, St. Croix, Sauk, Walworth, Waukesha, Waushara, and Winnebago counties.

1b. ASCLEPIAS INCARNATA ssp. **pulchra** (Ehrh.) Woodson, stat. nov.

Asclepias pulchra Ehrh. ex Willd. Sp. Pl. 1:1267. 1797, ex char.
Asclepias incarnata β pulchra (Ehrh.) Pers. Syn. 1:276. 1805.
Asclepias lasiotis Raf. Aut. Bot. 178. 1840, ex char.
Asclepias maritima Raf. loc. cit. 1840, ex char.
Asclepias incarnata var. *neoscotica* Fern. in Rhodora 23:288. 1921. [T.: *Fernald & Bissell 22318*, GH!]
Asclepias pulchra f. *albiflora* House, in Bull. N. Y. State Mus. 243–244:61. 1921, ex char. [T.: *Hollick s. n.*]
Asclepias incarnata var. *pulchra* f. *candida* Fern. in Rhodora 41:446. 1939. [Based on *A. pulchra* f. *albiflora* House].

Watersides and moist soil, frequently in somewhat brackish tidal marshes. Nova Scotia; Maine to South Carolina, adventive in Ohio, Florida, and Texas. Flowering from June to August.

CANADA: NOVA SCOTIA: Digby, Halifax, Lunenburg, and Yarmouth counties.

UNITED STATES:

CONNECTICUT: Fairfield, Hartford, New Haven, New London, Middlesex, and Windham counties.

DELAWARE: Kent, New Castle, and Sussex counties.

FLORIDA: Volusia County.

GEORGIA: Macon County.

MAINE: Androscoggin, Cumberland, Franklin, Kennebec, Lincoln, Oxford, Penobscot, Sagadahoc, Somerset, Washington, and York counties.

MARYLAND: Anne Arundel, Baltimore, Cecil, Harford, Prince Georges, and Worcester counties.

DISTRICT OF COLUMBIA.

MASSACHUSETTS: Barnstable, Berkshire, Bristol, Dukes, Essex, Hampden, Hampshire, Middlesex, Nantucket, Norfolk, Plymouth, Suffolk, and Worcester counties.

NEW HAMPSHIRE: Belknap, Carroll, Cheshire, Grafton, Hillsborough, Merrimack, Rockingham, and Strafford counties.

NEW JERSEY: Atlantic, Burlington, Camden, Cape May, Essex, Gloucester, Middlesex, Monmouth, Ocean, Salem, Somerset, and Union counties.

NEW YORK: Nassau, Richmond, Rockland, Suffolk, and Westchester counties.

NORTH CAROLINA: Alexander, Allegheny, Ashe, Beaufort, Burke, Caldwell, Caswell, Catawba, Cherokee, Currituck, Dare, Durham, Graham, Granville, Haywood, Henderson, Hertford, Lincoln, Macon, Mecklenberg, Mitchell, Orange, Rowan, Stanley, Union, Wake, and Wilkes counties.

OHIO: Lake County.

PENNSYLVANIA: Bucks, Chester, Delaware, Franklin, Lancaster, Montgomery, and Philadelphia counties.

RHODE ISLAND: Bristol, Kent, Newport, Providence, and Washington counties.

SOUTH CAROLINA: Anderson and Greenville counties.

TENNESSEE: Blount and Knox counties.

VERMONT: Caledonia and Windham counties.

VIRGINIA: Bedford, Fairfax, Floyd, James City, Princess Anne, Surry, and Sussex counties.

I interpret these two populations as allopatric subspecies because of the obvious genocline existing at the commissure of their natural distributions. This introgression lends itself to statistical analysis and was made a biometrical study by my friend and student, the late George K. Richardson, although still incomplete. From the unpublished data, it may be inferred that *A. i. incarnata* possibly spread northward and eastward from a refugium possibly in the Ozark upland at the retreat of glaciation, and that *A. i. pulchra* may have invaded the northeastern coastal plain from an ancestral home in the southern Appalachians subsequent to the last elevation of that upland and the retreat of the ice in the pattern made so familiar by Professor Fernald. At the present time, *A. i. pulchra* is frequent in more or less brackish lowlands roughly from the James estuary northeastward, and only occasional inland to elevations of approximately 2500 ft. in North and South Carolina.

2. ASCLEPIAS TEXANA Heller, Contr. Herb. Franklin & Marshall Coll., no. 1:77; *pl. 4.* 1895. [T.: *Heller 1859*, MO!]

Asclepias perennis var. *parvula* A. Gray, in Proc. Amer. Acad. 12:70. 1877. [T.: *Bigelow s. n.*, GH!]

Asclepias parvula (A. Gray) Vail, in Bull. Torrey Bot. Club 26:423. 1899.

Herbaceous perennials, becoming somewhat shrubby at the base after several years. Stems slender, 2–4 dm. tall, usually branching only at the base, inconspicuously pilosulose in decurrent lines from the nodes. Leaves opposite, petiolate, broadly oval to narrowly oblong-elliptic, acuminate, obtuse or rarely attenuate at the base, 2–7 cm. long, 0.7–2.5 cm. broad, thinly membranaceous, finely puberulent upon the midrib and veins beneath; petioles 0.5–1.0 cm. long, minutely pilosulose. Inflorescences solitary at the uppermost nodes, several- to many-flowered; peduncles slender, 1–2 cm. long; pedicels 1.0–1.3 cm. long, finely puberulent. Flowers small; calyx lobes narrowly lanceolate, 1.5–2.0 mm. long, minutely puberulent; corolla reflexed-rotate, white, the lobes about 3 mm. long, widely spreading; gynostegium long-stipitate, white, the column cylindric, about 1.5 mm. long and 0.7 mm. wide at the base, the hoods cucullate, about 2 mm. long, rounded at the tip, the horn basal, narrowly acicular, nearly twice as long as the hood, slightly incurved over the anther head, the anther head about 2.5 mm. long. Follicles erect on erect pedicels, narrowly fusiform, 9–12 cm. long, smooth, glabrous; seeds broadly oval, about 8 mm. long, the white coma about 2 cm. long.

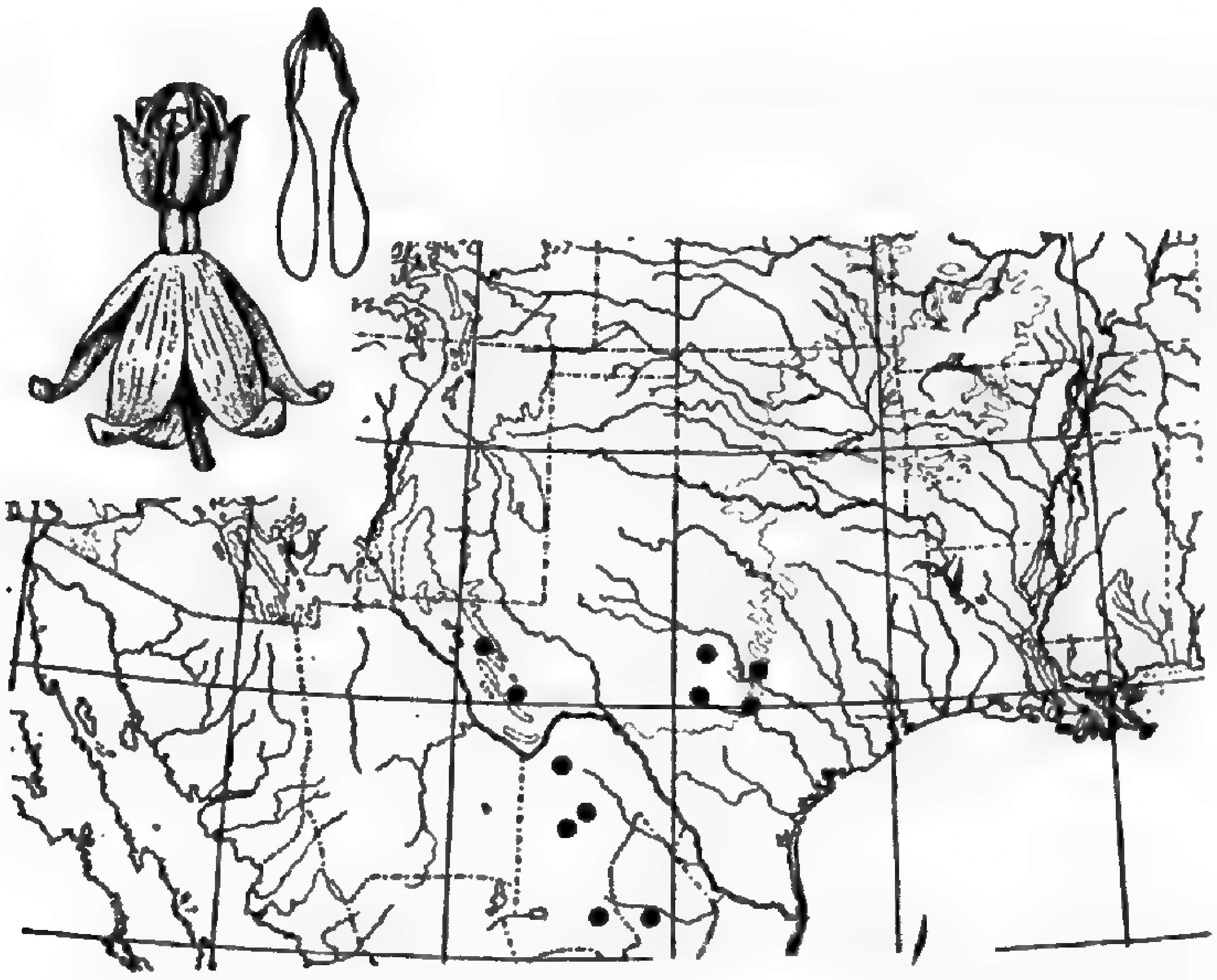

Fig. 8. *Asclepias texana* Heller

Canyons and arroyos. Southwestern Texas; Nuevo Leon and Coahuila. Flowering from June to August.

UNITED STATES:
TEXAS: Brewster, Comal, Jeff Davis, Kerr, Llano, and Travis counties.

MEXICO: COAHUILA: Saltillo, Villa Acuña, Monclova, Muzquiz, Cuatro Cienagas. NUEVO LEÓN: Monterrey.

I cannot distinguish *A. texana* from *A. perennis* except by means of the strikingly different fruit and seed, and the geographical distribution.

3. ASCLEPIAS PERENNIS Walt. Fl. Carol. 107. 1788, ex char.

Asclepias parviflora Ait. Hort. Kew. 1:307. 1789, ex char.
Asclepias pulchella Salisb. Prodr. 150. 1796, ex char.
Asclepias debilis Michx. Fl. Bor.-Amer. 1:116. 1803, ex char.
Asclepias parviflora Ait. var. *latifolia* Raf. Aut. Bot. 179. 1840, ex char.
Asclepias lancifolia Raf. loc. cit. 177. 1840, ex char

Herbaceous perennials from rather short and superficial root-stalks. Stems slender, 3–5 dm. tall, usually branching only from the base, very inconspicuously pilosulose in decurrent lines from the nodes, or essentially glabrous. Leaves opposite, narrowly oblong to broadly oval or ovate-elliptic, acuminate, attenuate at the base, 5–14 cm. long, 0.5–1.5 cm. broad, thinly membranaceous, glabrous; petioles 0.5–1.5 cm. long. Inflorescences solitary at the uppermost nodes, several- to many-flowered; peduncles slender, 1–4 cm. long; pedicels 1.0–1.3 cm. long, usually somewhat suffused with purple. Flowers small; calyx lobes oblong-elliptic, about 1 mm. long, sparsely and minutely pilosulose; corolla reflexed-rotate, white usually suffused with pale pink, the lobes 3–4 mm. long; gynostegium stipitate, white, the column cylindric, about 1 mm. long and wide, the hoods cucullate, rounded at the tip, about 2 mm. long, slightly longer than the anther head, the horn basal, narrow-acicular, somewhat longer than the hoods, slightly arching over the anther head. Follicles pendulous on deflexed peduncles, rather broadly ovoid-fusiform with a rather long apical beak, 4–7 cm. long, 1.0–2.5 cm. broad, smooth, glabrous; seeds broadly oval, about 1.5 cm. long, without a coma.

Low swampy ground, frequently with bald cypress; alluvial woods, sloughs, and ditches. South Carolina to Florida and westward to eastern Texas, up the lower Mississippi Valley to southern Missouri, Illinois, and southwestern Indiana. Flowering from April to September.

ALABAMA: Tuscaloosa County.

ARKANSAS: Clay, Craighead, Crittenden, Desha, Drew, Jackson, Mississippi, Poinsett, Prairie, Pulaski, Randolph, and St. Francis counties.

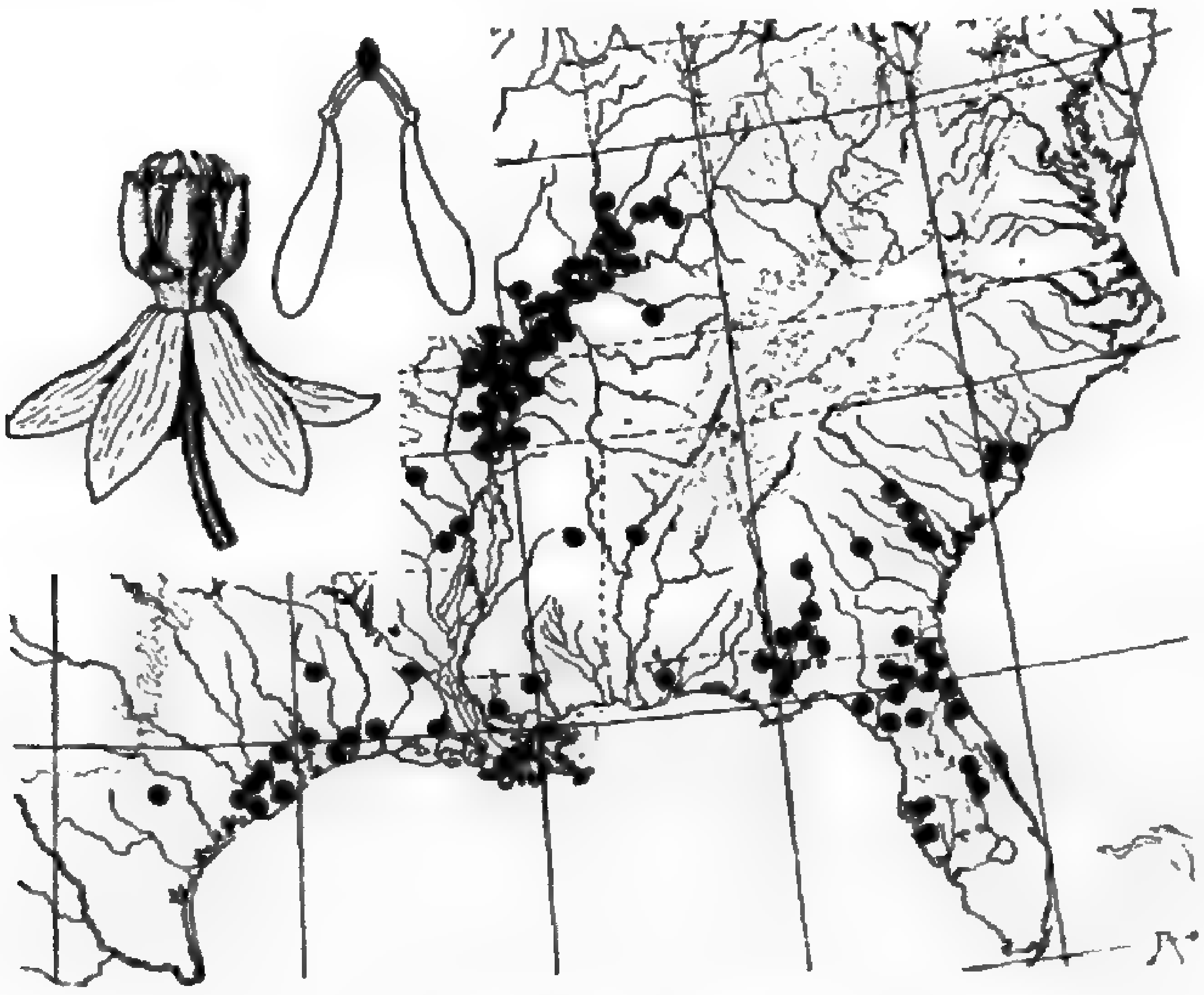

Fig. 9. *Asclepias perennis* Walt.

FLORIDA: Alachua, Columbia, Dixie, Duval, Escambia, Flagler, Gadsden, Hillsborough, Jackson, Levy, Liberty, Manatee, Marion, Nassau, Orange, Osceola, Putnam, St. Johns, and Union counties.

GEORGIA: Baker, Burke, Charlton, Dougherty, Jenkins, Laurens, Macon, Miller, Screven, and Thomas counties.

ILLINOIS: Alexander, Gallatin, Jackson, Johnson, Lawrence, Pope, Pulaski, Union, Wabash, Wayne, and White counties.

INDIANA: Dubois, Gibson, Jackson, Knox, Lawrence, Pike, Posey, Spencer, Sullivan, and Warrick counties.

KENTUCKY: Ballard, Carlisle, Henderson, Hickman, McCracken, Union, and Warren counties.

LOUISIANA: Calcasieu, Jefferson, Lafayette, Lafourche, Livingston, Orleans, Rapides, Terre Bonne, and Washington parishes.

MISSISSIPPI: Oktibbeha County.

MISSOURI: Butler, Dunklin, Ripley, and Wayne counties.

SOUTH CAROLINA: Berkeley, Georgetown, and Williamsburg counties.

TENNESSEE: Dyer and Shelby counties.

TEXAS: Angelina, Brazoria, Dallas, Fort Bend, Harns, Jackson, Jefferson, Liberty, Matagorda, Orange, and Wharton counties.

The peculiar pendulous follicles and large naked seeds would appear to be a striking adaptation to dissemination by water, but similar fruit and seed characters of *Asclepias pellucida* and *A. humilis* are associated with very different habitats (highland pine, fir, and oak forests; rocky meadows).

4. ASCLEPIAS WOODSONIANA Standl. & Steyermark, in Field Mus. Publ. Bot. 23:224. 1947. [T.: *Steyermark 31781*, MO!]

Herbaceous perennials. Stems rather slender, 1–4 dm. tall, usually branching only from the base, very inconspicuously pilosulose in decurrent lines from the nodes or essentially glabrous. Leaves opposite, very shortly petiolate, narrowly lanceolate to linear-lanceolate, very gradually acuminate, the base typically more or less hastate-revolute, 5–17 cm. long, 3–12 mm. broad, membranaceous, glabrous or very inconspicuously pilosulose on the midrib beneath; petioles 1–3 mm. long. Inflorescences solitary at the uppermost nodes; peduncles 2–5 cm. long; pedicels 0.7–1.3 cm. long. Flowers small; calyx lobes lance-trigonal, about 2.5 mm. long; corolla reflexed-rotate, greenish white, the lobes about 5 mm. long; gynostegium white, stipitate, the column cylindric, about 1 mm. long and broad, the hoods cucullate, about 2 mm. long, the basal horns nearly twice as long as the hood, narrowly acicular and gradually incurved over the anther head, the anther head about 2 mm. long and broad. Follicles erect on erect pedicels, narrowly fusiform, 8–10 cm. long, about 5 mm. broad; seeds oval, about 7 mm. long, the coma about 2.5 cm. long.

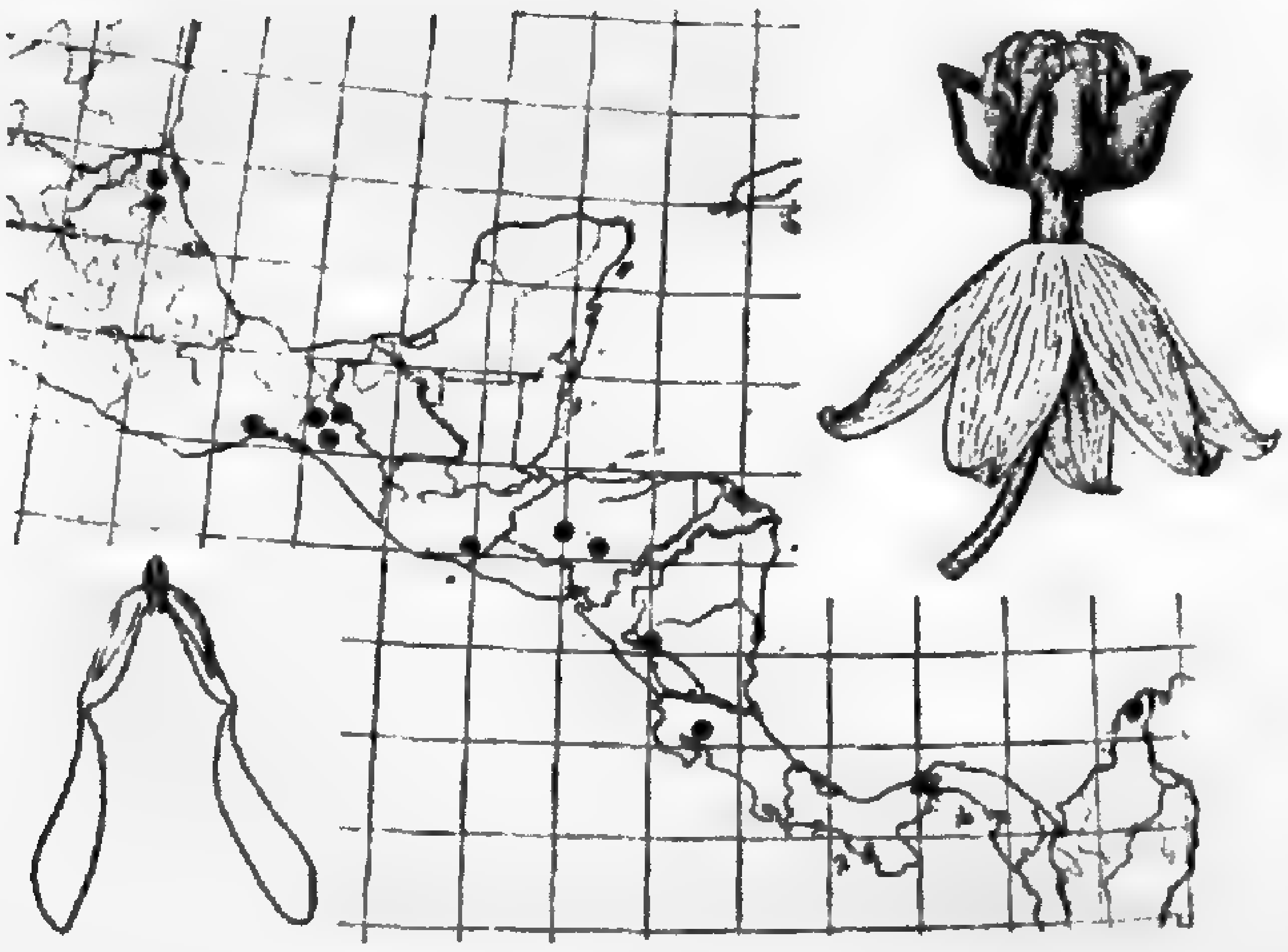

Fig. 10. *Asclepias woodsoniana* Standl. & Steyerm.

Meadows, occasionally pine-oak forest, thorn scrub, and salt flats, from near sea level to 1000 m. elevation. Southern Mexico to western Costa Rica. Flowering from March to August.

MEXICO: CHIAPAS: San Richardo and Ocozucuantla. OAXACA: San Mateo del Mar. VERACRUZ: Guayabo, Rancho La Palmilla, Cuitlahuac, Santa María.

GUATEMALA: JUTIAPA: Trapiche Vargas and Asunción Mita.

HONDURAS: EL PARAÍSO: Galeras, Las Casitas. MORAZÁN: Río Yeguare, Las Mesas, Maraíta.

EL SALVADOR: AHUACHAPÁN: Ahuachapán. CHALATENAGO. LA UNION: Amatillo.

NICARAGUA: MANAGUA: Managua.

COSTA RICA: GUANACASTE: La Cruz.

This species, so well distinguished by the narrow, hastate-revolute leaves, also appears to have been collected near Puerto Colómbia, Colómbia, by Brother Elías (*Elías 1028* in Herb. Chicago Nat. Hist. Mus.).

5. Asclepias linearis Scheele, in Linnaea 21:758. 1848. [T.: *Lindheimer 456*, MO!]

Asclepias verticillata var. *linearis* (Scheele) Pollard, in Bull. Torrey Bot. Club 24:156. 1897.

Herbaceous perennials from rather short and superficial rootstalks. Stems slender, 2–5 dm. tall, usually branching only at the base, inconspicuously pilosulose in decurrent lines from the nodes. Leaves opposite, sessile or subsessile, linear, 3–9 cm. long, 1–4 mm. broad, membranaceous, glabrous or minutely puberulent along the midrib beneath. Inflorescences solitary at several or many of the upper nodes, several-flowered; peduncles slender, 1.0–1.5 cm. long; pedicels 5–7 mm. long. Flowers small; calyx lobes lance-trigonal, about 2 mm. long, minutely puberulent; corolla reflexed-rotate, greenish white, the lobes 3–4 mm. long; gynostegium long-stipitate, white, the column cylindric, about 1 mm. long and 0.5 mm. broad, the hoods cucullate, subquadrate, about 1.5 mm. long, the basal horn narrowly acicular, somewhat longer than the hood, gradually arching over the anther head; anther head about 1.5 mm. long and slightly narrower. Follicles erect on erect pedicels, narrowly fusiform, 5–10 cm. long, smooth, glabrous; seeds broadly oval, about 5 mm. long, the white coma about 2 cm. long.

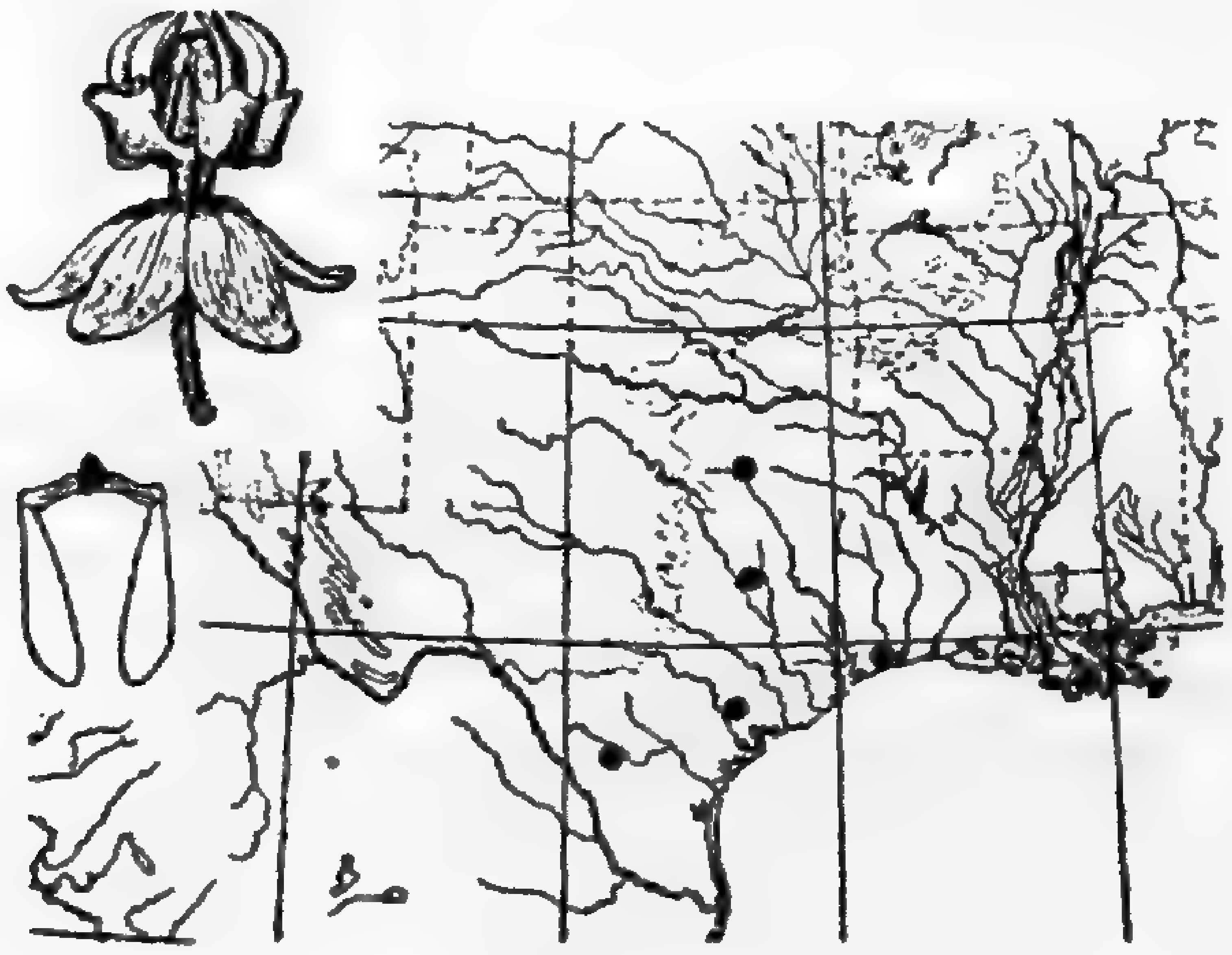

Fig. 11. *Asclepias linearis* Scheele

Dry prairies. South-central Texas. Flowering from May to September.

United States:
texas: Dallas, Jefferson, LaSalle, Milam, and Victoria counties.

This infrequently collected population is still something of an enigma to me, and I have been inclined at times to treat it as an opposite-leaved variety or subspecies of *A. verticillata*, as did Pollard. However, the species of Series incarnatae as a whole show great floral uniformity and are distinguished habitually by vegetative characters which frequently are rather slight. Such being the case, and with its coherent distribution and apparent lack of intergradation, I am maintaining *A. linearis* as a species.

6. ASCLEPIAS **pseudorubricaulis** Woodson, spec. nov.

Herbae perennes ex caudice parvo radicibus numerosis fibrosis carnosis. Caules graciles simplices vel subsimplices 1.5–7.0 dm. alti in lineas minute pubescentes e nodis decurrentes caeterumque glabri. Folia opposita linearia subsessilia 6–10 cm. longa 1–3 mm. lata revoluta glabra. Inflorescentiae ad nodos subterminales solitariae vel terminales multiflorae congestae; pedunculo 1.5–2.5 cm. longo sparse pilosulo; pedicellis ca. 1 cm. longis pilosulis. Flores inter species generis parvissimi; calycis laciniis anguste trigonalibus ca. 2 mm. longis inconspicue pilosulis; corolla reflexe rotata pallide purpurea lobis ca. 4 mm. longis; gynostegio anguste stipitato albido, columna cylindrica ca. 1 mm. longo paullum minus lato, cucullis subquadratis minute sed distincte stipitatis ca. 1.25 mm. longis cornu basi adnato aciculari cucullo ca. bis longiore supra androecium leviter inflexo, androecio cylindrico ca. 1.5–1.75 longo et lato. Folliculi erecti pedunculo pedicello erectis anguste fusiformes ca. 6–9 cm. longi ca. 5 mm. lati laeves glabri; seminibus ovalibus ca. 5 mm. longis, coma alba ca. 2.5 cm. longa.

MEXICO: TAMAULIPAS: 25 mi. s. of Matamoras, *Wooton s. n.* (US). SAN LUIS POTOSÍ: between San Tiburcio and Angostura, *Purpus 5217* (F. GH. MO(HOLOTYPE), NY, UC, US); Minas de San Rafael, *Purpus 5569* (UC); Las Tablas, *Pennell 18054* (US).

Like nearly all other INCARNATAE except *A. curassavica* and *A. gentryi*, this species is distinguished by rather subtile differences of habit rather than the dramatic floral characters characteristic of the species of other series and subgenera.

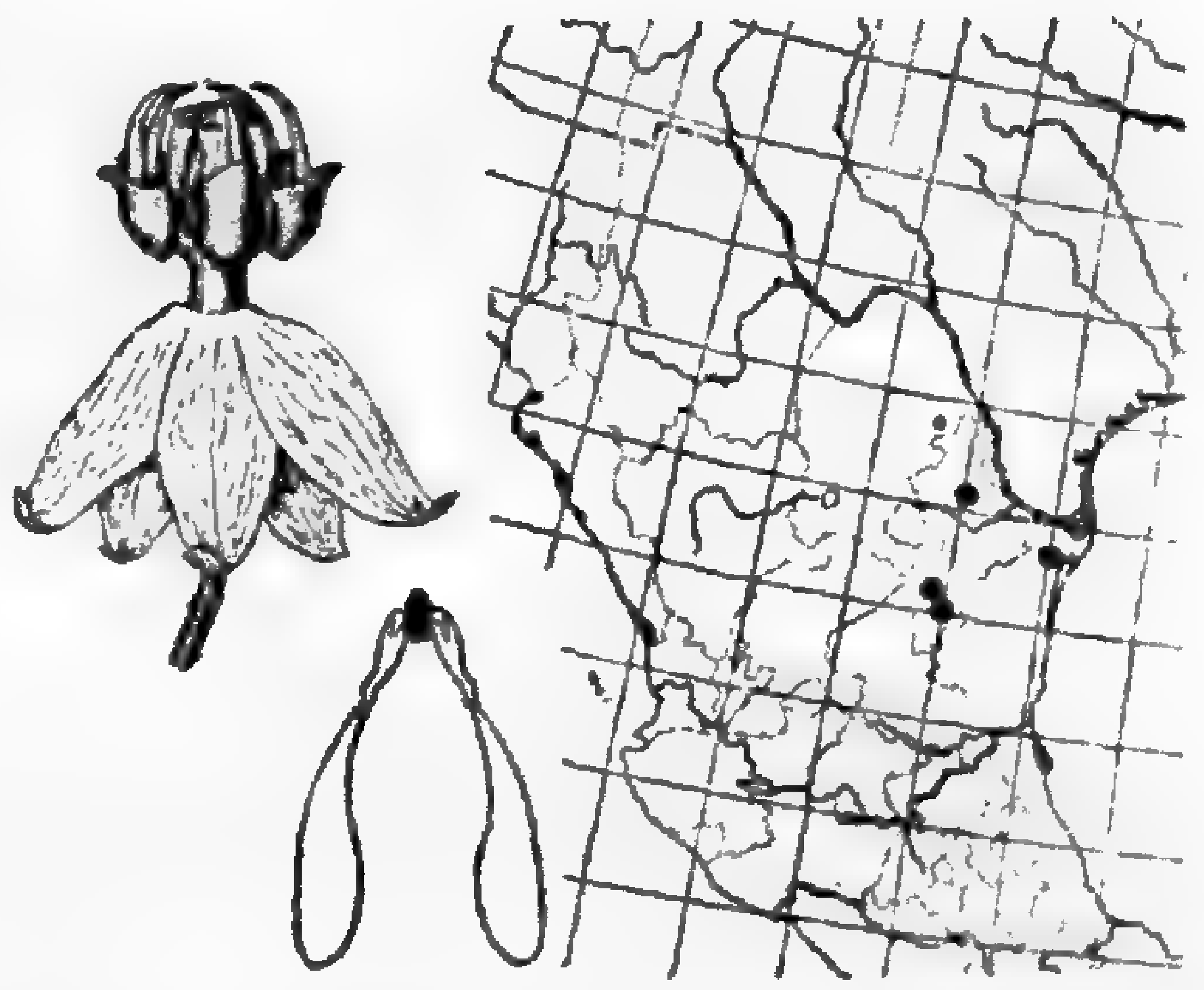

Fig. 12. *Asclepias pseudorubricaulis* Woods.

7. ASCLEPIAS CURASSAVICA L. Sp. Pl. 215. 1753. [T.: Linn. Herb. London, no. *310.19*, photo!]

Asclepias bicolor Moench, Meth. 717. 1794, ex char.
Asclepias aurantiaca Salisb. Prodr. 150. 1796, nom nud.
Asclepias margaritacea Hoffmgg. ex Roem. & Schult. Syst. 6:86. 1820, ex char. [T.: *Hoffmannsegg s. n.*]
Asclepias cubensis Wender, in Bot. Zeit. 1:830. 1843, ex char.
Asclepias nivea var. *curassavica* (L.) O. Ktze. Rev. Gen. 1:418. 1891.
Asclepias curassavica var. *concolor* Kr. & Urb. in Urb. Symb. Ant. 1:389. 1899. [T.: *Sintennis 3949*, MO!]

Herbaceous annuals. Stems 3–12 dm. tall, frequently rather woody toward the base, simple or branched, minutely arachnoid-tomentulose when young, soon

Fig. 13.
Asclepias curassavica L.

glabrate. Leaves opposite, petiolate, elliptic-lanceolate, acute to acuminate, the base acute to obtuse, 5–12 cm. long, 1–3 cm. broad, minutely pilosulose when very young, soon glabrate, thinly membranaceous; petioles 0.5–1.0 cm. long. Inflorescences solitary at the upper nodes, several- to many-flowered; peduncles 3–6 cm. long; pedicels 1–2 cm. long. Flowers rather large and showy; calyx lobes narrowly lanceolate, 2–3 mm. long; corolla reflexed-rotate, bright crimson, rarely yellow or white, the lobes 5–10 mm. long; gynostegium long-stipitate, deep yellow, the column cylindric or conic, 2–3 mm. long and 1 mm. broad at the base, the hoods cucullate, distinctly stipitate, broadly oblong, rounded at the tip, 3–5 mm. long, the horn basal, narrowly acicular, 4–5 mm. long, slightly incurved over the anther head; anther head cylindrical, 2–3 mm. long, 1.5–2.5 mm. broad. Follicles erect on erect pedicels, narrowly fusiform, 6–10 cm. long, smooth, glabrous; seeds broadly oval, 5–7 mm. long, the white coma about 2–3 cm. long.

Almost ubiquitous waifs of the tropics and subtropics of the Americas, frequenting chiefly rather moist places at elevations from near sea-level to about 2000 m.; also widely introduced in the tropics of the Old World. Blooming sporadically throughout the year.

The native home of *A. curassavica* is quite conjectural. It is so named from Linnaeus' belief that its provenience is Curaçao; whether it is the Antilles, Mexico and Central America, or even southern South America appears quite impossible of solution. I am of the opinion that it is South American, although Sir Hans Sloane reported it widespread in Jamaica. In the southern United States the species has appeared as occasional ruderals in southern California, Florida, Louisiana, and Texas.

The species is so widespread and so familiar that it appears unnecessary to provide special data of its distribution.

Putative hybrids of *A. curassavica* × *nivea* from Jamaica have been described by Urban (Symb. Ant. 1:388. 1899).

8. Asclepias nivea L. Sp. Pl. 215. 1753, ex ic. cit.

Asclepias nivea α normalis O. Ktze. Rev. Gen. 2:418. 1891, ex char.
Asclepias nivea β flava O. Ktze. loc. cit. 1891, ex char.
Asclepias nivea var. *intermedia* Schltr. in Urb. Symb. Ant. 1:244. 1899. [T.: *Harris 5276*, MO!]

Herbaceous annuals. Stems rather slender, 1–5 dm. tall, usually branching only from the base, generally puberulent when young, becoming glabrate. Leaves ovate to lanceolate-elliptic, apex acuminate, base acute to obtuse, 5–15 cm. long, 1–4 cm. broad, thinly membranaceous, rather inconspicuously puberulent on both surfaces, frequently glabrate above; petioles 0.5–1.5 cm. long. Inflorescences solitary at a few of the uppermost nodes, few- to several-flowered; peduncle 1.3–5.0

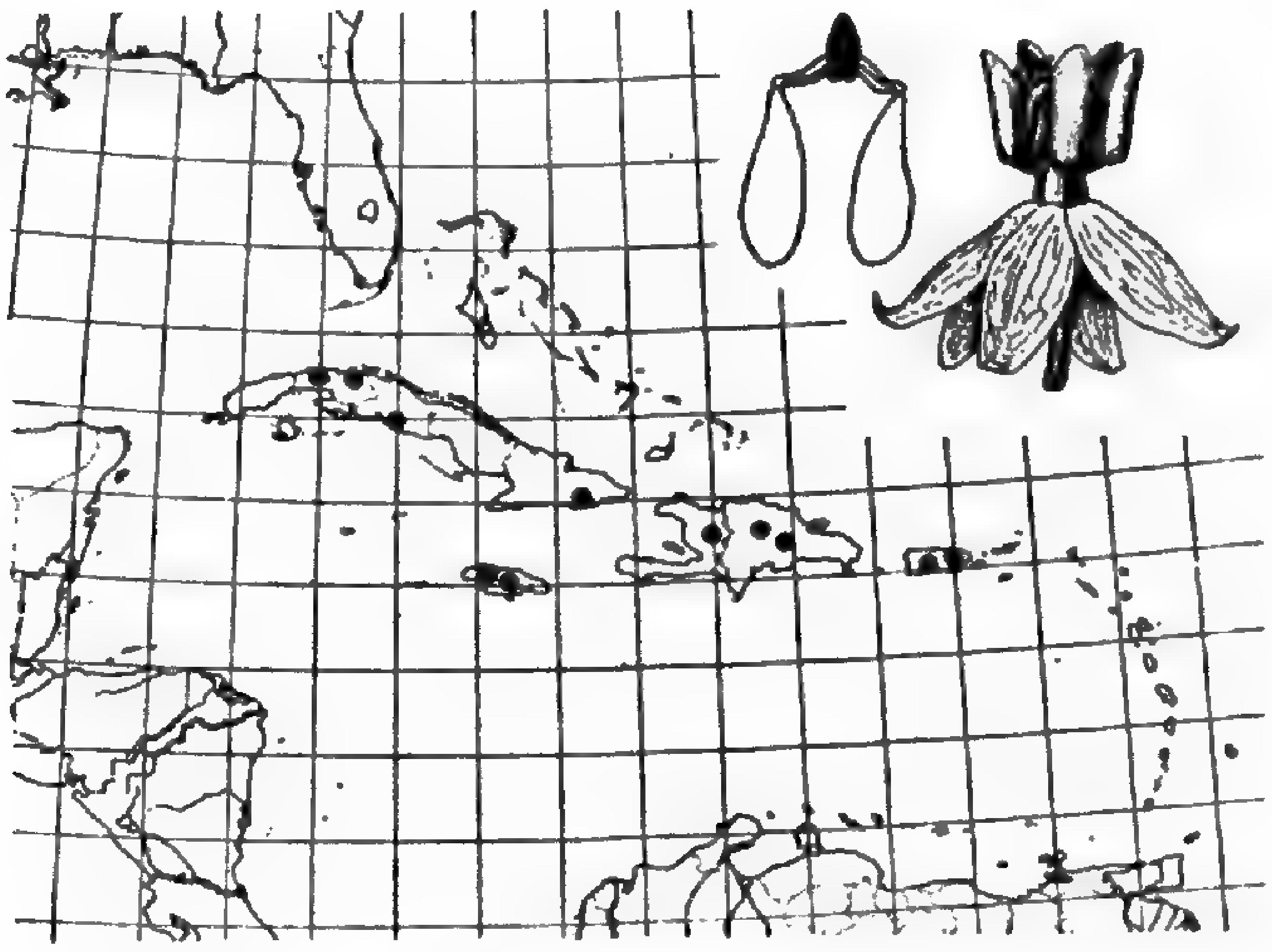

Fig. 14. *Asclepias nivea* L.

cm. long; pedicels slender, 1.0–1.8 cm. long. Flowers rather small; calyx lobes narrowly trigonal, about 2.5 mm. long, inconspicuously puberulent; corolla reflexed-rotate, pale green or greenish white, the lobes about 6 mm. long; gynostegium rather shortly stipitate, white, the column about 1 mm. long and broad, the hoods cucullate, rather narrowly oblong, shortly stipitate, about 3 mm. long, the horn slightly longer than the hood and arching over the anther head, the anther head cylindrical, about 2 mm. long and 1.4 mm. broad. Follicles erect on erect pedicels, narrowly fusiform, smooth, glabrous, 5–7 cm. long, about 6 mm. thick; seeds oval, about 5 mm. long, the white coma 1.5–2.0 cm. long.

Thickets and stream sides. Cuba, Jamaica, Hispaniola, and Puerto Rico. Flowering sporadically throughout the year.

CUBA: SANTA CLARA: Cienfuegos, Soledad. HABANA: Havana. MATANZAS: Matanzas.
JAMAICA: Farm Hill, Bog Walk, Moy Hall.
DOMINICAN REPUBLIC: San José de las Matas, Juan Santiago.
HAITI: St. Michel de l'Atalaye.
PUERTO RICO: Ciales, Ponce, Las Mesas.

Asclepias curassavica and *A. nivea* appear so distinct to me that I cannot understand the confusion and doubt which has surrounded them. The distinguishing characters as I view them are contained in the previous key to species. The species are so distinct, in fact, that I am rather skeptical of the reported hybrids.

In the Linnean Herbarium at London there are two specimens (nos. *310.21,* and *310.22* labelled *Asclepias nivea.* Both are in fact specimens of *A. variegata* L., as shall be explained presently. There is no specimen of the population traditionally named *A. nivea* in the herbarium of Linnaeus.

In his description of *A. nivea* Linnaeus is quite enigmatic, but cites two unillustrated polynomials of Gronovius and Plumier and also an illustrated reference to Dillenius. The habit given is *"in Virginia & America calidiore"*, suspicious at face value. The Gronovius reference may well apply to *A. variegata* and may explain the presence of the two sheets presently representing *A. nivea* in the

Linnaean Herbarium. The reference to Plumier, although rather sketchy, is sufficient to indicate the tropical American provenience of his plant. That to Dillenius (Dill. Hort. Elth. 1:33. *t. 32.* 1732) is virtually without doubt our *Asclepias nivea:* his extended description of *Apocynum persicariae mitis folio corniculis lacteis* is replete with detail obviously compiled from living plants, and the excellent full-page illustration of the plant in both flower and fruit quite closes the case.

Linnaeus, therefore, obviously included two quite separate elements under his *Asclepias nivea:* one coinciding with our present-day *A. variegata* and the other with *A. nivea* of present usage. Paradoxically, in the Linnaean Herbarium there is no specimen of *A. variegata* labelled as such by either Linnaeus or his son. Beside the two specimens of *A. variegata* labelled as *A. nivea* there is a third sheet of the species labelled *dilatata,* a manuscript name.

Were it not for the fact that Linnaeus' description of *A. variegata* is so explicit (viz. "*floribus albis intus purpureis*" which is incapable of confusion with any other species!), the matter might be more difficult of solution. As matters stand, I would suggest Linnaean Herb. no. *310.20* (*A. dilatata* ms.) as lectotype for *A. variegata,* and Dill. Hort. Elth. 1:33. *t. 32.* 1732) *in lieu* of type for *A. nivea.* This will leave the practical applications of the names precisely where they stand but upon a somewhat better understanding of sources.

9. Asclepias angustifolia Schweig. Enum. Pl. Hort. Bot. Regiomont. 13. 1812, ex char.

Asclepias virgata Balb. Cat. Hort. Taur. 14. 1813, ex char.
Asclepias salicifolia Lodd. Bot. Cab. 3:*t. 272.* 1818, non Salisb., ex ic.
Asclepias rubricaulis HBK. Nov. Gen. 3:189. 1819, ex char. [T.: *Bonpland 3919.*]
Asclepias linifolia HBK. loc. cit. 190. 1819. [T.: *Bonpland s. n.,* P photo!]
Asclepias linifolia Lag. ex Spreng. Syst. 1:847. 1825, ex char.
Asclepias longifolia Sessé & Moc. Fl. Mex. 2:72. 1894. [T.: *Sessé & Mociño 1283,* F!]
Asclepias angustifolia Sessé & Moc. loc. cit. 1894. [T.: *Sessé & Mociño 1284,* F!]
Asclepias jaliscana M. E. Jones, Contr. West. Bot. 12:49. 1908, non Robins. [T.: *Jones s. n.,* MO!]
Asclepias tapalpana M. E. Jones, loc. cit. 14:35. 1912. [Based on *A. jaliscana* M. E. Jones.]

Herbaceous, usually somewhat suffrutescent annuals. Stems 1.5–8.0 dm. tall, slender, simple or repeatedly branching, minutely puberulent in decurrent lines from the nodes, eventually glabrate. Leaves opposite, shortly petiolate, linear to linear-lanceolate, acuminate, acute to attenuate at the base, 3–15 cm. long, 0.2–1.5 cm. broad, firmly membranaceous, frequently somewhat revolute, inconspicuously pilosulose beneath to wholly glabrous. Inflorescences solitary at rather few upper nodes, few- to several-flowered; peduncle 1–2 cm. long; pedicels 1.0–1.5 cm. long. Flowers small; corolla reflexed-rotate, white, rarely pink, the lobes 4–5 mm. long; gynostegium white, stipitate, the column cylindrical, about 1 mm. long and broad, the hoods cucullate, oblong, distinctly stipitate, 3–4 mm. long, the horn basal, narrowly acicular, slightly longer than the hood, gradually arching over the anther head, the anther head cylindric, about 2 mm. long and broad. Follicles erect on

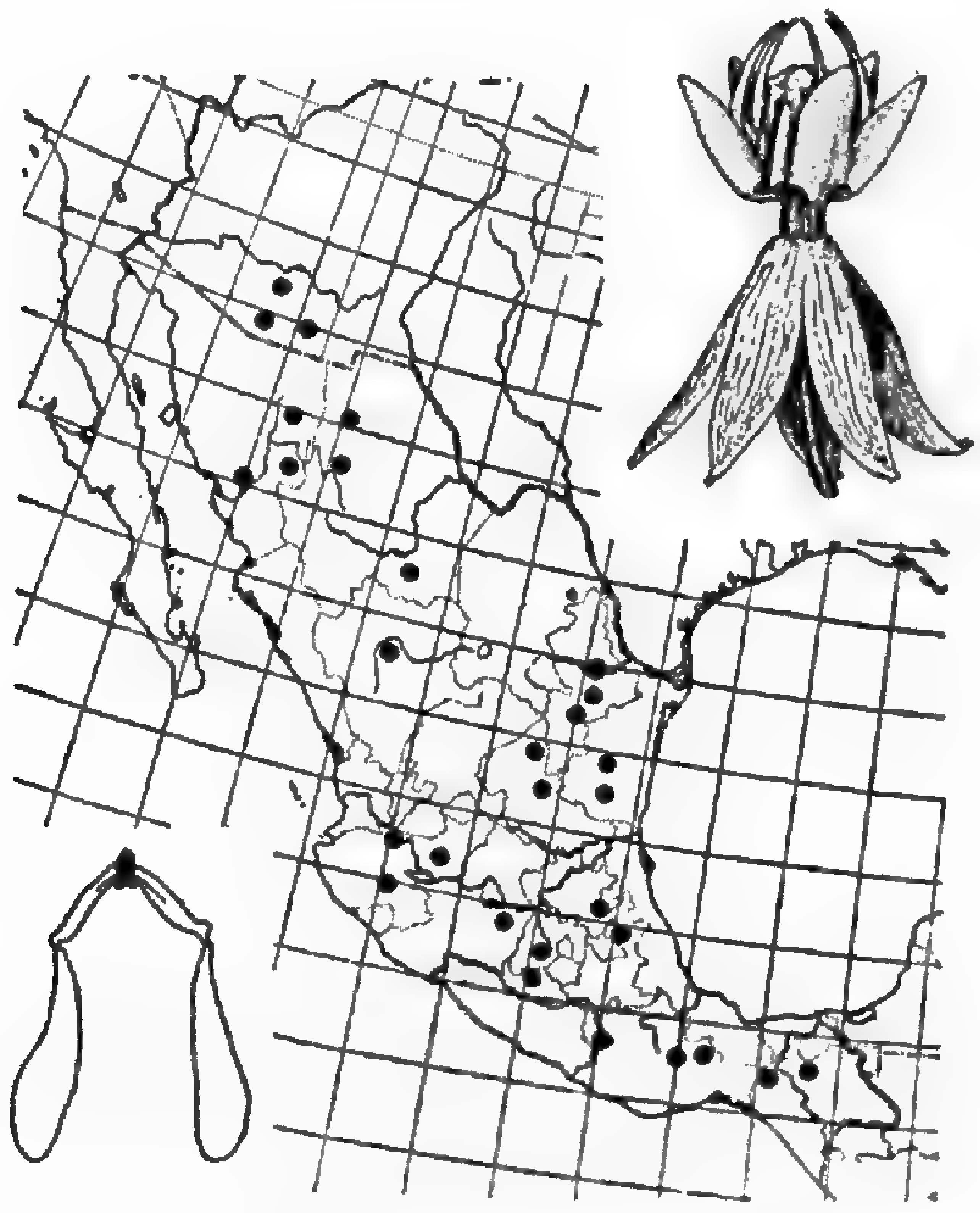

Fig. 15. *Asclepias angustifolia* Schweig.

erect pedicels, narrowly fusiform, about 6–10 cm. long and 5–8 mm. thick, smooth, essentially glabrous; seeds oval, 5–6 mm. long, the white coma 1.5–3.0 cm. long.

Creek bottoms, canyons, and arroyos. Southern Arizona; Tamaulipas to Sonora and southward to Chiapas. Flowering sporadically throughout the year.

UNITED STATES:

ARIZONA: Cochise, Pima, and Santa Cruz counties.

MEXICO: CHIAPAS: San Ricardo, Ocozucuantla. CHIHUAHUA: Galleana, Sierra Charuco, Tosanachic, Colonia Díaz. DURANGO: Tobar. GUERRERO: Taxco. HIDALGO: Huejutla. JALISCO: Chiquilistlán, Sierra de Nayarit, Sierra de la Campaña, Guadalajara. MEXICO: Temascaltepec. MICHOACAN: Morelia. NUEVO LEON: Monterrey, Villa de Santiago, Dulces Nombres. OAXACA: Tlaxiaco, Yavezia, Misteca Alta, Chicahuastla. PUEBLA: Puebla. SAN LUIS POTOSÍ: San Luis Potosí, Las Canoas. SONORA: Bavispe, Alamos, Cañon de El Tremblor. TAMAULIPAS: San José, Victoria, Jaumave.

This is a very frequent species in the Mexican uplands. Interpretation of Schweigger's and Balbis' names is based not so much on the brief original diagnoses as on specimens bearing the names which are deposited in the Bernhardi Herbarium of the Missouri Botanical Garden. These plants probably were grown in Bernhardi's garden at Erfurt at about the time of publication of their names, and quite possibly came from seed from the original plants. The type specimen of *A. rubricaulis*, although cited by Fournier (Ann. Sci. Nat. Ser. VI, 14:376. 1882), cannot now be found at the Paris herbarium. *Galeotti 1617*, also cited for *A. rubricaulis* by Fournier, is rather widely represented in European and American herbaria, however, and is the basis for my association of the name with *A. angustifolia* Schweig.

10. **Asclepias fascicularis** Dcne. in DC. Prodr. 8:569. 1844. [T.: *Douglas s.n.* K photo!]

Asclepias macrophylla Nutt. in Jour. Acad. Phila. Ser. II, 1:180. 1847. [T.: *Nuttall s. n.*, BM photo!]
Asclepias macrophylla var. *comosa* Dur. & Hilg. in Rept. Expl. Pacific R. R. Surv. 5:370. *t. 8.* 1856, ex ic.
Asclepias fasciculata Hemsl. Biol. Centr.-Am. Bot. 2:324. 1882, sphalm.

Herbaceous perennials from rather stout woody rootstalks. Stems 4–10 dm. tall, almost invariably with numerous microphyllous axillary branches, rarely simple, usually more or less puberulent in decurrent lines from the nodes, frequently glabrate. Leaves predominantly 3-nate or 4-nate upon the flowering stems, shortly petiolate, oblong- to linear-lanceolate, acuminate to obtuse at the tip, acute to obtuse at the base, 3–12 cm. long, 0.1–2.5 cm. broad, membranaceous, glabrous to inconspicuously pilosulose beneath, those of the sterile dwarf branches opposite and much reduced, giving the plants a heterophyllous appearance; petioles 1–3 mm. long. Inflorescences paired or clustered at the uppermost nodes, several- to many-flowered; peduncle rather slender, 2–4 cm. long; pedicels slender, 0.7–1.5 cm. long. Flowers rather small; calyx lobes narrowly trigonal, 1.0–1.5 mm. long, pilosulose to glabrate; corolla reflexed-rotate, usually grayish pink, infrequently white, the lobes 3–4 mm. long; gynostegium narrowly stipitate, grayish pink or white, the column cylindric, about 1 mm. long and broad, the hoods cucullate, oval, about 1.0–1.5 mm. long, the horn basal, narrowly acicular, about half longer than the hood, gradually arching over the anther head, the anther head cylindric, about 1.5 mm. long and broad. Follicles erect on erect pedicels, narrowly fusiform, about

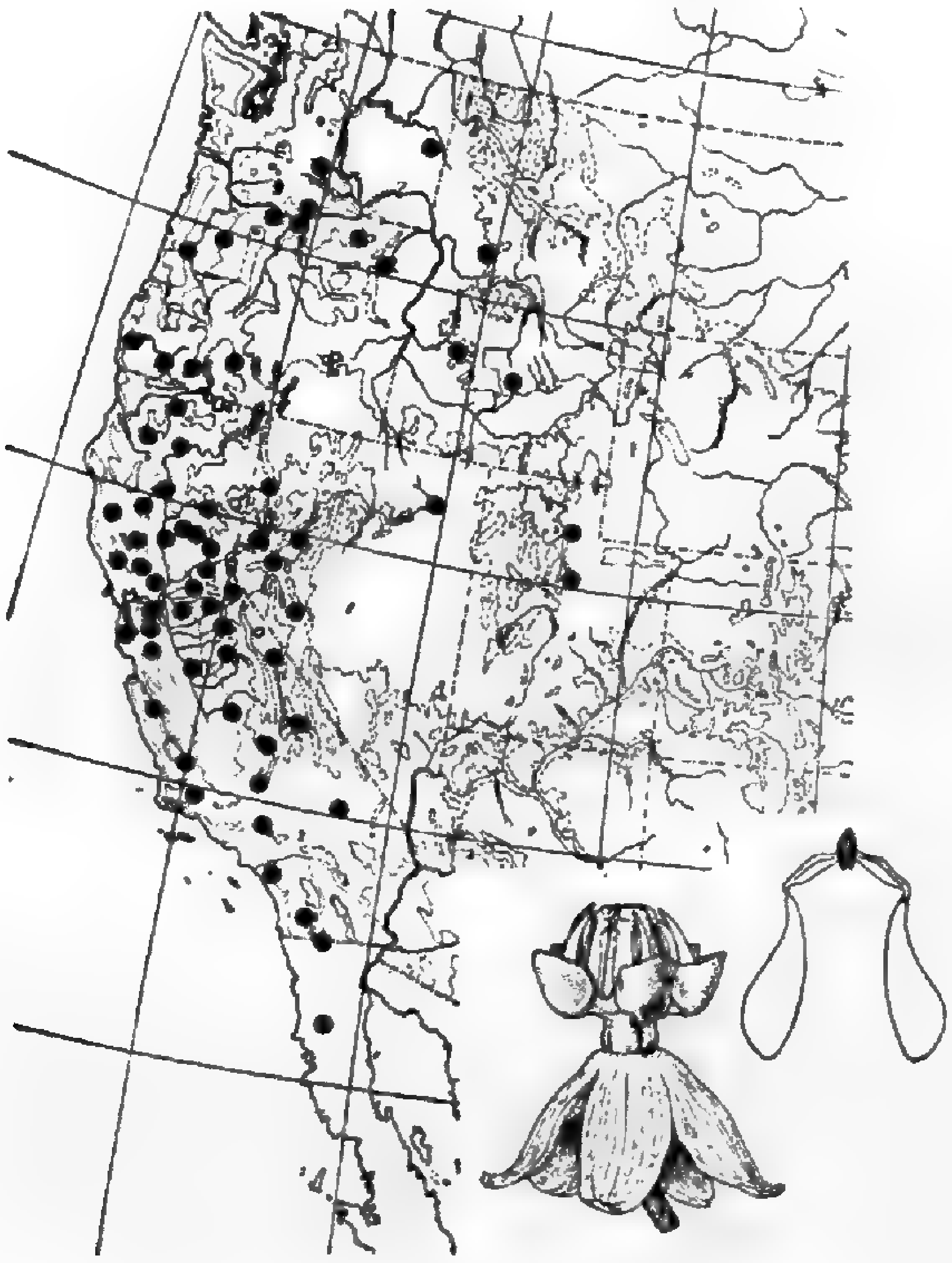

Fig. 16. *Asclepias fascicularis* Dcne.

5–12 cm. long and 0.7–1.0 cm. thick, smooth, glabrous; seeds oval, 6–7 mm. long, the white coma about 2 cm. long.

Plains, hills, and valleys, in moist or dry soil; spreading to roadsides and waste places; regarded as poisonous to stock. Idaho, Utah, and Nevada westward to the Pacific Coast; northern Baja California. Flowering from May to October.

United States:

CALIFORNIA: Alameda, Alpine, Amador, Butte, Calaveras, Contra Costa, Eldorado, Fresno, Glen, Inyo, Kern, Lake, Los Angeles, Mariposa, Mendocino, Merced, Mono, Monterey, Napa, Orange, Placer, Plumas, San Bernardino, San Diego, San Joaquin, San Luis Obispo, San Mateo, Santa Barbara, Santa Clara, Shasta, Siskiyou, Solano, Sonoma, Sutter, Tehama, Trinity, Tulare, Tuolumne, and Yuba counties.

IDAHO: Adams, Blaine, Boise, Idaho, Owyhee, and Washington counties.

NEVADA: Churchill, Elko, Lyon, Mineral, Storey, and Washoe counties.

OREGON: Benton, Curry, Hood River, Jackson, Josephine, Klamath, Marion, Wasco, Union, and Umatilla counties.

UTAH: Davis and Utah counties.

WASHINGTON: Klickitat, Spokane, and Yakima counties.

Mexico: BAJA CALIFORNIA: Vallecitos, Monument No. 245, San Ysidro.

This is the "*Asclepias mexicana*" of most American authors. Durand & Hilgard's plate *(vide ante)* is an excellent one, and illustrates the dwarf sterile branches with their reduced opposite leaves in fine detail. Similarly, Cavanilles' plate of his *A. mexicana* (Ic. 1:*t. 58.* 1791) is quite as good for the latter species. I suppose that the confusion has been due in part to our failure to appreciate the systematic importance of the presence or absence of the microphyllous branches, and in part to the scarcity of herbarium specimens of the true *A. mexicana.*

The verticillate-leaved species of INCARNATAE form a most interesting *artenkreiss* which I assume to have originated from *A. incarnata.* Certainly it would be very difficult to distinguish *A. fascicularis* from *A. incarnata* except for the phyllotaxy if the two species possessed a common distribution. *A. fascicularis* is essentially a western *A. incarnata.* As it extends to the southeast, however, it gradually merges into *A. subverticillata* throughout the southern Great Basin area. In turn, as *A. subverticillata* reaches the Great Plains, it is replaced by *A. verticillata,* which extends on to the Atlantic coast. *Asclepias mexicana* might be visualized as a vicariad extending southward in the Mexican upland, and *A. pumila* as an offshoot northward in the western Great Plains.

The most closely related units of this *artenkreiss,* say *A. fascicularis* and *A. subverticillata,* might be interpreted as subspecies of a single species if viewed separately. Yet any adjacent members of the series are similarly related, and it would be unthinkable to associate the end members within a single species, as *A. incarnata* or *A. verticillata,* for example.

11. Asclepias subverticillata (A. Gray) Vail, in Bull. Torrey Bot. Club 25:178. 1898.

Asclepias verticillata var. *subverticillata* A. Gray, in Proc. Am. Acad. 12:71. 1877. [T.: *Wright 1685,* MO!]

Herbaceous perennials from rather stout, woody rootstalks. Stems 1.5–12 dm. tall, almost invariably with sterile, dwarf, microphyllous branches, occasionally simple, more or less puberulent in decurrent lines from the nodes, occasionally quite glabrous. Leaves predominantly 3-nate to 5-nate but occasionally opposite above on the flowering stems, shortly petiolate, linear, 2–13 cm. long, 1–4 mm. broad, membranaceous, glabrous to inconspicuously pilosulose, those of the sterile dwarf branches opposite and much reduced and giving the plant a heterophyllous aspect; petioles 1–2 mm. long. Inflorescences usually solitary at the upper nodes, rarely paired, several- to many-flowered; peduncle slender, 1.5–3.0 cm. long; pedicels slender, 5–8 mm. long. Flowers relatively small; calyx lobes narrowly trigonal, 1.5–2.0 mm. long, inconspicuously pilosulose to glabrate; corolla reflexed-rotate, white, rarely slightly suffused with greenish purple, the lobes 3–5 mm. long; gynostegium narrowly stipitate, white, the column cylindrical, about 1 mm. long and slightly narrower, the hoods cucullate, oval, about 1.5 mm. long, the horn basal, narrowly acicular, somewhat longer than the hoods, gradually arching over the anther head; anther head cylindric, about 1.5 mm. long and broad. Follicles erect on erect pedicels, narrowly fusiform, about 5–9 cm. long and 6–8 mm. thick, smooth, glabrous or inconspicuously pilosulose; seeds broadly oval, 7–8 mm. long, the white coma about 2 cm. long.

Sandy and rocky plains and flats; very poisonous to stock. Arizona, New Mexico, southern Utah and Colorado, western Texas; northern Mexico from Nuevo León to Sonora. Flowering from June to August.

United States:
arizona: Apache, Cochise, Coconino, Gila, Navajo, Pima, Pinal, and Yavapai counties.

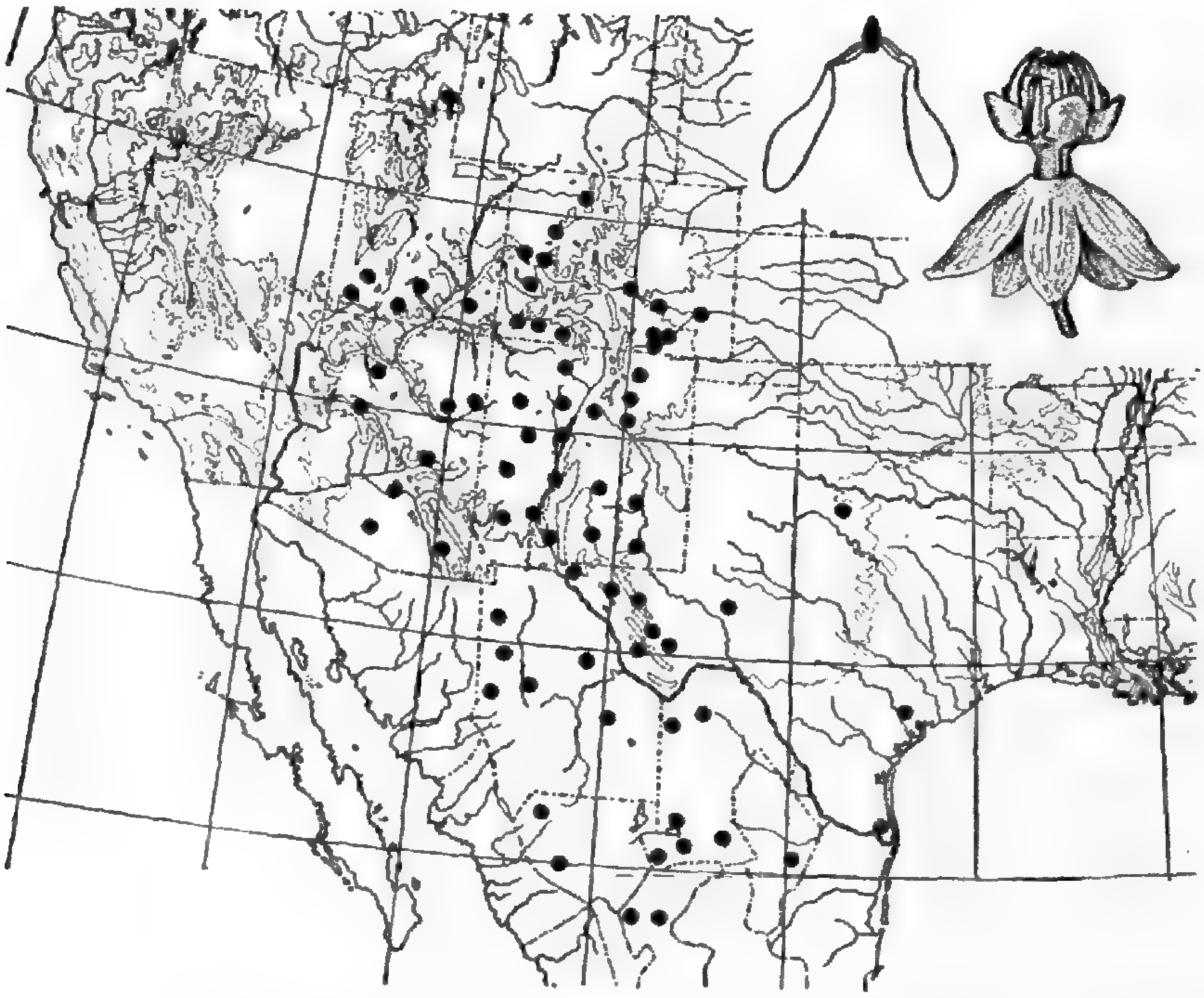

Fig. 17. *Asclepias subverticillata* (Gray) Vail

Colorado: Archuleta, Bent, Crowley, Delta, Fremont, Garfield, La Plata, Larimer, Las Animas, Mesa, Montezuma, Otero, Pueblo, and Routt counties.

Idaho: Bear Lake County.

New Mexico: Bernalillo, Catron, Chaves, Colfax, Dona Ana, Eddy, Grant, Lincoln, McKinley, Otero, Rio Arriba, Sandoval, San Miguel, Santa Fe, Sierra, Socorro, and Valencia counties.

Texas: Archer, Brewster, Cameron, Culberson, El Paso, Hudspeth, Jeff Davis, Presidio, Upton, and Victoria counties.

Utah: Garfield, Iron, Kane, San Juan, and Washington counties.

Mexico: Chihuahua: Chihuahua, Villa Ahumada, Carretas, Cd. Camargo, Colonia Díaz. Coahuila: Saltillo, Parras, Castillon, San Lorenzo de Laguna, Puertecito, La Ventana, Avalos, Torreón, Americanos. Durango: Tepehuanes, Durango, Nombre de Dios, Bermejillo, Villa Juárez. Nuevo León: Galeana. Sonora: San Pedro, El Potrero.

This is the "*Asclepias galioides*" of most American authors. Gray's var. *subverticillata* was based upon Torrey's *A. verticillata* var. *galioides* as to specimens cited, amongst which I am choosing *Wright 1685* as the lectotype, since it exemplifies the species well and is represented in numerous herbaria. *A. subverticillata* is further discussed under *A. fascicularis*. True *A. galioides* HBK. is merely a narrow-leaved variant of *A. mexicana* Cav.

12. **Asclepias mexicana** Cav. Ic. 1:42. *t. 58.* 1791. [T.: Herb. Cav., MA!]

Asclepias galioides HBK. Nov. Gen. 3:188. 1819. [T.: *Bonpland 4304*, P photo!]
Asclepias verticillata var. *α galioides* (HBK.) Fourn. Ann. Sci. Nat. Ser. VI, 14:375. 1882 (ascribed to Kunth).
Asclepias verticillata var. *β mexicana* (Cav.) Fourn. loc. cit. 1882.

Herbaceous perennials. Stems rather slender, 2–7 dm. tall, simple and homophyllous, very rarely with sterile, dwarf, microphyllous branches toward the base, inconspicuously puberulent in thin decurrent lines from the nodes, or essentially glabrous. Leaves chiefly 4-nate to 6-nate, shortly petiolate, elliptic to narrowly elliptic-lanceolate, apex acute to acuminate, base acute to obtuse, 2–13 cm. long, 1.5–15 mm. broad, firmly membranaceous, scatteringly pilosulose beneath to essentially glabrous, frequently somewhat revolute; petioles 1–8 mm. long. Inflorescences paired or clustered at the uppermost nodes, rather many-flowered; peduncle 1–5 cm. long; pedicels slender, 0.8–1.2 cm. long. Flowers rather small; calyx lobes narrowly elliptic, rather inconspicuously pilosulose, 2.5–3.0 mm. long; corolla reflexed-rotate, white but usually more or less suffused with purple, the lobes about 5 mm. long; gynostegium narrowly stipitate, white, the column cylindric, 1 mm. long and broad, the hoods cucullate, oval, 2.0–2.5 mm. long, the basal horn narrowly acicular, somewhat longer than the hood and gradually arching over the

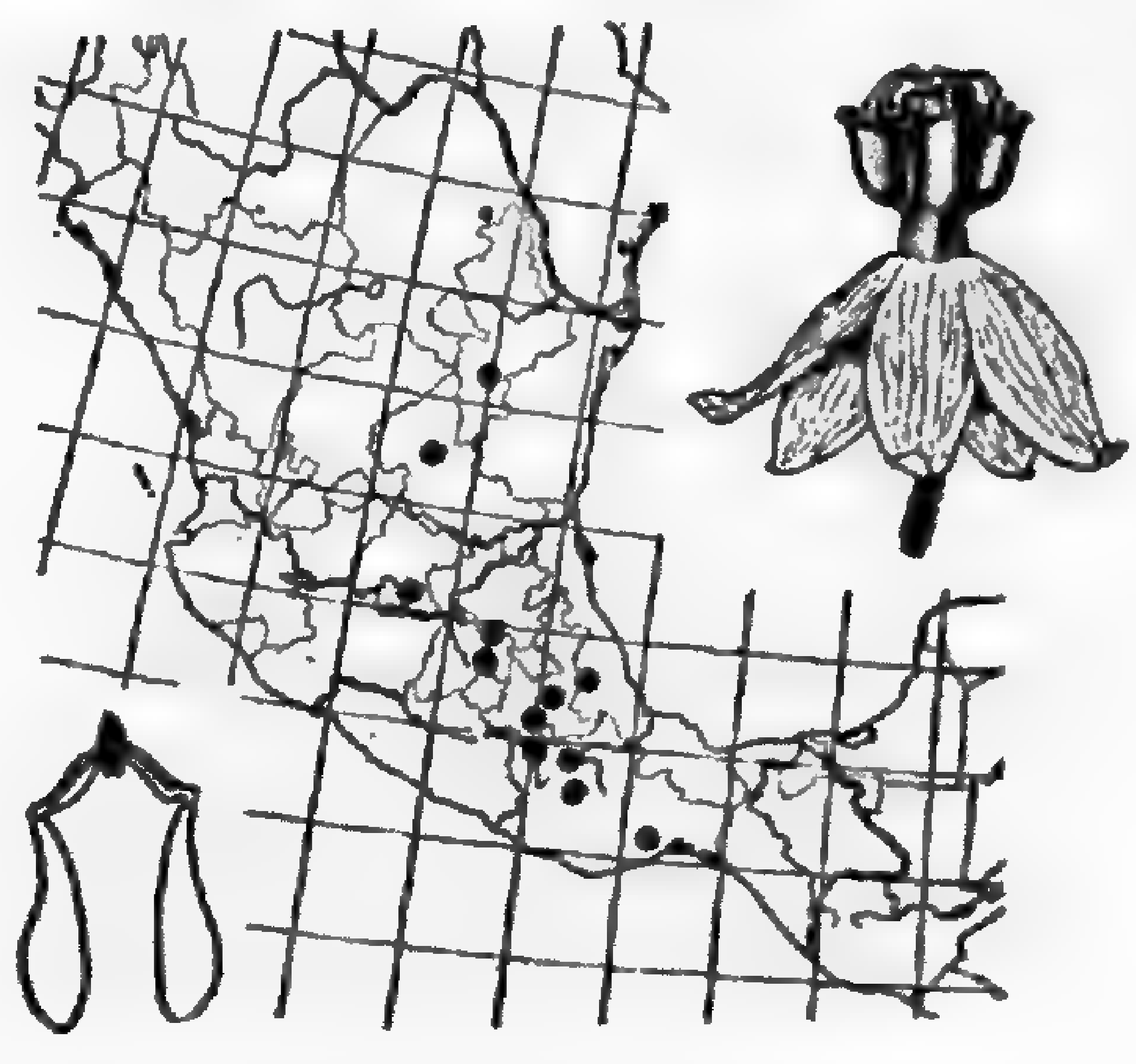

Fig. 18. *Asclepias mexicana* Cav.

anther head, the anther head cylindric, about 1.5–2.0 mm. long and broad. Follicles erect on erect pedicels, narrowly fusiform, about 7–10 cm. long and 5–8 mm. thick, smooth, essentially glabrous; seeds broadly oval, 4–5 mm. long, the white coma 2.0–3.5 cm. long.

Wet meadows and marshes, spreading to scrub and waste places; central Mexico. Flowering from May to November.

Mexico: distrito federal: Valley of Mexico. guanajuato: León. mexico: Tlalnepantla. nuevo león: Galeana. oaxaca: Cerro Verde, Etla, San Miguel Quilitongo, Chicahuastla. pueblo: Rancho Posadas, Guadalupe. san luis potosí: San Luis Potosí. veracruz: Acultzingo.

Extremely variable in the size and width of the leaves, *A. mexicana* appears to be a vicariad of *A. incarnata* of the eastern United States, not only in natural relationship but in habitat preference.

13. **Asclepias verticillata** L. Sp. Pl. 217. 1753. [T.: Linn. Herb. London, no. *310.38*, photo!]

Asclepias parviflora Leconte, ex Dcne. in DC. Prodr. 8:570. 1844, nom. nud. in synon.

Herbaceous perennials from rather short, superficial rootstalks. Stems slender, 1.5–9.0 dm. tall, simple, or rarely with short sterile branches, more or less puberulent in decurrent lines from the nodes, rarely glabrate. Leaves chiefly 3-nate or 4-nate, rarely opposite in part, sessile or subsessile, linear, 1.5–7.0 cm. long, about 1.5 mm. broad, membranaceous, glabrous or essentially so, usually somewhat revolute. Inflorescences solitary or paired at the upper nodes, few- to many-flowered; peduncles slender, 1.5–3.0 cm. long; pedicels slender, 6–8 mm. long. Flowers small; calyx lobes narrowly trigonal, 1.5–2.5 mm. long, sparsely pilosulose to glabrous; corolla reflexed-rotate, greenish white occasionally somewhat flushed with purple without, the lobes about 3.5 mm. long; gynostegium narrowly stipitate, greenish white, the column narrowly cylindrical, about 1 mm. long and somewhat narrower, the hoods cucullate, subquadrate, about 1.5 mm. long, the basal horn narrowly acicular, about twice as long as the hood and arching gradually over the anther head, the anther head cylindrical, about 2 mm. long and somewhat narrower. Follicles erect on erect pedicels, narrowly fusiform, 7–10 cm. long and 5–8 mm. thick, smooth, glabrous; seeds oval, about 5 mm. long, the white coma about 2.5 cm. long.

Prairies, thickets, and open woods, usually in rather dry soil; sand-dunes; spreading to roadsides and fence corners. Southern Ontario and Manitoba; Massachusetts to Florida and westward to North Dakota and Texas. Flowering from April to August.

Canada: manitoba: Emerson and St. Boniface counties. ontario: Essex, Norfolk, and Welland counties.

United States:

alabama: Barbour, Houston, Lee, Mobile, and Tuscaloosa counties.

arkansas: Baxter, Benton, Carroll, Garland, Johnson, Marion, Miller, Montgomery, Prairie, Pulaski, Scott, Washington, and Yell counties.

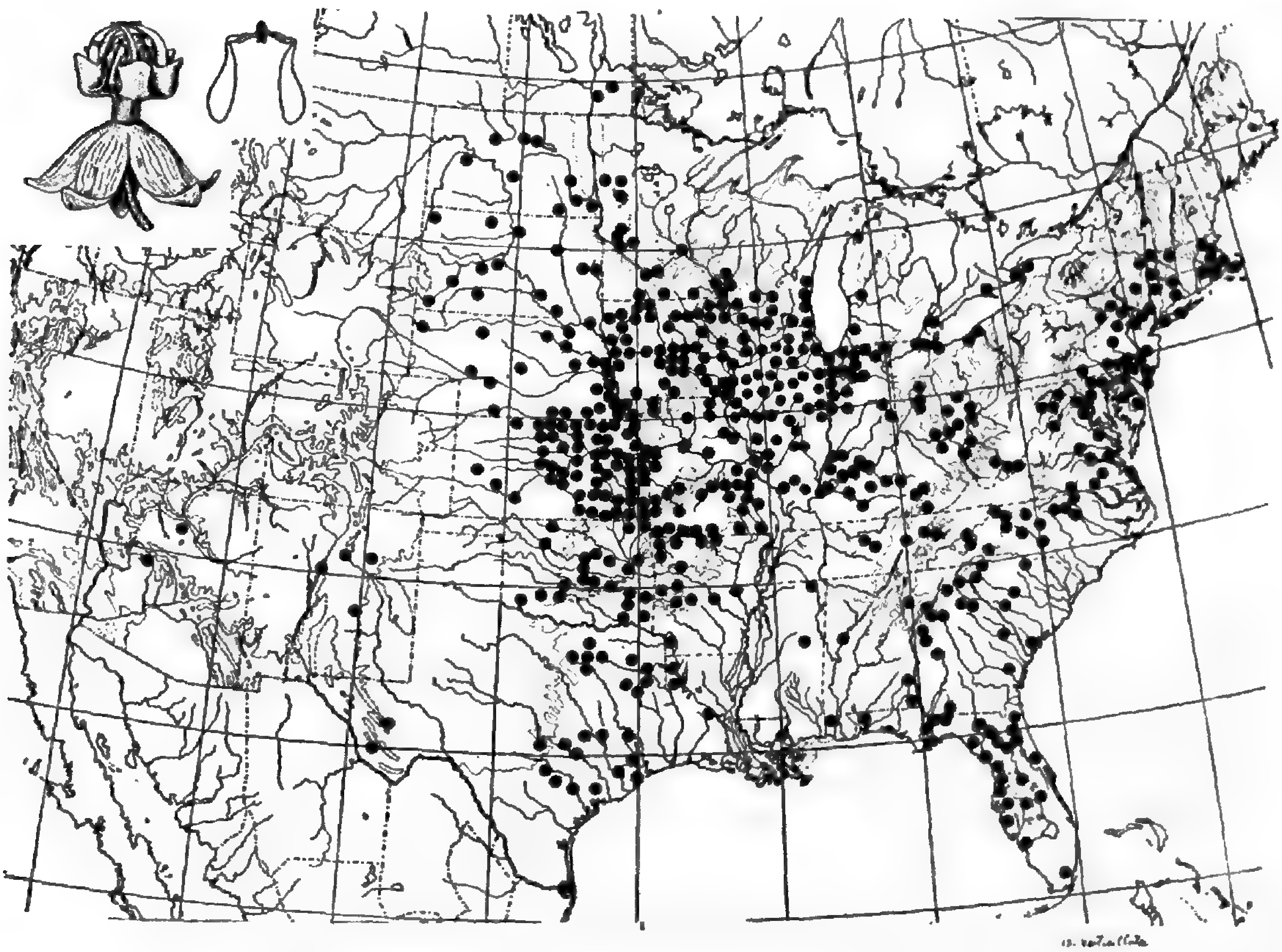

Fig. 19. *Asclepias verticillata* L.

CONNECTICUT: Hartford and New Haven counties.

DELAWARE: Kent, New Castle, and Sussex counties.

FLORIDA: Alachua, Citrus, Clay, Dade, Dixie, Duval, Franklin, Gadsden, Hernando, Hillsborough, Lake, Lee, Leon, Levy, Liberty, Manatee, Marion, Osceola, Pasco, Polk, Putnam, Santa Rosa, Suwanee, and Volusia counties.

GEORGIA: Clarke, Cobb, Coweta, DeKalb, Floyd, Fulton, Hall, Jenkins, Long, Meriwether, Oglethorpe, Richmond, Stephens, Taylor, and Thomas counties.

ILLINOIS: Adams, Bureau, Carroll, Cass, Champaign, Christian, Cook, DeKalb, Douglas, Edgar, Effingham, Fayette, Ford, Hancock, Iroquois, Jackson, Kankakee, Knox, LaSalle, Lee, Livingston, Logan, McDonough, McLean, Macon, Macoupin, Madison, Mason, Menard, Ogle, Peoria, Piatt, Pope, Putnam, Richland, St. Clair, Stark, Union, Vermilion, Will, Witt, and Woodford counties.

INDIANA: Benton, Cass, Clark, Clinton, Crawford, Daviess, Delaware, Elkhart, Fulton, Gibson, Harrison, Jasper, Knox, Kosciusko, LaGrange, Lake, LaPorte, Marshall, Miami, Montgomery, Newton, Noble, Orange, Perry, Porter, Pulaski, St. Joseph, Spencer, Starke, Steuben, Tippecanoe, Vermillion, Warren, Wayne, and White counties.

IOWA: Allamakee, Black Hawk, Boone, Carroll, Cerro Gordo, Cherokee, Chickasaw, Clay, Clayton, Clinton, Crawford, Dallas, Decatur, Des Moines, Dickinson, Emmet, Fayette, Floyd, Greene, Guthrie, Harrison, Henry, Ida, Jackson, Johnson, Lee, Linn, Madison, Mahaska, Muscatine, Marshall, Monona, O'Brien, Page, Palo Alto, Polk, Pottawattamie, Poweshiek, Sioux, Story, Union, Van Buren, Wapello, Warren, Winneshiek, Woodbury, and Wright counties.

KANSAS: Allen, Anderson, Atchison, Barton, Butler, Chase, Chautauqua, Cherokee, Clay, Cloud, Cowley, Crawford, Dickinson, Doniphan, Douglas, Finney, Ford, Franklin, Geary, Greenwood, Harvey, Jackson, Jewell, Johnson, Labette, Leavenworth, Lincoln, Linn, Lyon, McPherson, Marshall, Miami, Montgomery, Morris, Nemaha, Neosho, Norton, Osage, Osborne, Ottawa, Phillips, Pottawatomie, Reno, Republic, Riley, Rooks, Rush, Saline, Sedgwick, Shawnee, Smith, Stafford, Sumner, Wabaunsee, Washington, Wichita, and Wyandotte counties.

KENTUCKY: Edmonson, Henderson, Lewis, Mercer, Nelson, Ohio, Pulaski, Rockcastle, Union, Warren, and Whitley counties.

LOUISIANA: Caddo, DeSoto, Rapides, and Saint Tammany counties.

MARYLAND: Baltimore, Caroline, Carroll, and Montgomery counties.

MASSACHUSETTS: Barnstable, Bristol, Franklin, Middlesex, Norfolk, Plymouth, and Suffolk counties.

MICHIGAN: Kent and Van Buren counties.

MINNESOTA: Becker, Brown, Chippewa, Clay, Faribault, Houston, Jackson, Kandiyohi, Mower, Nicollet, Otter Tail, Pope, Ramsey, Swift, and Winona counties.

MISSISSIPPI: Alcorn and Oktibbeha counties.

MISSOURI: Atchison, Barry, Barton, Boone, Butler, Cass, Cedar, Dent, Franklin, Gentry, Greene, Hickory, Holt, Iron, Jackson, Jasper, Jefferson, Knox, Laclede, Linn, Madison, McDonald, Oregon, Ozark, Pike, Phelps, Pulaski, Ralls, Reynolds, St. Francois, St. Louis, Saline, Scotland, Stone, Taney, Washington, and Worth counties.

NEBRASKA: Antelope, Cass, Cherry, Custer, Dodge, Douglas, Gage, Holt, Jefferson, Keith, Knox, Lancaster, Lincoln, Nemaha, Nuckolls, Otoe, Platte, Red Willow, Richardson, Sioux, Washington, and Webster counties.

NEW JERSEY: Atlantic, Burlington, Camden, Cape May, Cumberland, Gloucester, Passaic, Salem, and Somerset counties.

NEW YORK: Albany, Columbia, Dutchess, Nassau, Niagara, Rensselaer, Rockland, Suffolk, and Ulster counties.

NORTH CAROLINA: Alexander, Ashe, Buncombe, Durham, Forsyth, Granville, Madison, Montgomery, Orange, Polk, Randolph, Rowan, Wake, and Wilkes counties.

NORTH DAKOTA: Barnes, Benson, Dickey, Dunn, Pierce, Ransom, Richland, and Ward counties.

OHIO: Adams, Athens, Clark, Cuyahoga, Erie, Fairfield, Greene, Jackson, Lake, Logan, Lucas, Meigs, Ottawa, Ross, and Scioto counties.

OKLAHOMA: Alfalfa, Cherokee, Cleveland, Comanche, Craig, Creek, Garvin, Grady, Hughes, Jackson, Latimer, Le Flore, Logan, McCurtain, Major, Miami, Muskogee, Oklahoma, Ottawa, Payne, Pottawatomie, and Pushmataha counties.

PENNSYLVANIA: Adams, Berks, Chester, Delaware, Lackawanna, Lancaster, Luzerne, Monroe, and Pike counties.

RHODE ISLAND: Kent and Providence counties.

SOUTH CAROLINA: Aiken, Anderson, Beaufort, Greenville, Lancaster, and Lexington counties.

SOUTH DAKOTA: Brookings, Brule, Charles Mix, Clay, Corson, Fall River, Haakon, Harding, Kingsbury, Pennington, Spink, Stanley, Walworth, and Washabaugh counties.

TENNESSEE: Anderson, Cumberland, Davidson, Knox, and Rutherford counties.

TEXAS: Anderson, Bastrop, Bexar, Brazos, Cameron, Cherokee, Dallas, Denton, De Witt, Fort Bend, Galveston, Gillespie, Gregg, Harris, Jackson, Jeff Davis, Johnson, Milam, Parker, Presidio, Rusk, Tarrant, Travis, Walker, Wilson, and Wood counties.

VIRGINIA: Arlington, Bedford, Campbell, Essex, Greensville, James City, Loudoun, Louisa, Mecklenburg, Prince William, Princess Anne, Shenandoah, and Sussex counties.

WEST VIRGINIA: Cabell, Grant, Hampshire, Hardy, Monroe, Raleigh, Summers, and Wayne counties.

WISCONSIN: Columbia, Crawford, Dane, Grant, Green, Kenosha, La Crosse, Lafayette, Milwaukee, Ozaukee, Sauk, Sheboygan, Trempealeau, and Walworth counties.

Superficially one of the most homogenous of species, *A. verticillata,* none the less, shows an interesting geographical variation in the margin of the minute corona hoods: the more eastern populations have hoods with rather sharp marginal lobes; but toward the west, where the species approaches the range of *A. sub-*

verticillata, the marginal lobes become broader and less prominent in the manner of the more simple oval hoods of the latter species (and in fact of all other species of INCARNATAE). This variation, which may indicate introgression of *A. verticillata* with *A. subverticillata,* could be measured rather precisely and probably would lend itself nicely to biometric analysis.

14. ASCLEPIAS PUMILA (A. Gray) Vail, in Britton & Brown, Illustr. Fl. 3:12. 1898.

Asclepias verticillata var. *pumila* A. Gray, in Proc. Amer. Acad. 12:71. 1877. [T.: *Fendler* 45, MO!]

Herbaceous perennials from rather deep rootstalks. Stems cespitose from the crown, simple or branching infrequently below ground level, relatively slender, 0.5–3.0 dm. tall, minutely puberulent generally. Leaves spirally approximate and very crowded or the lowest occasionally verticillate, sessile, filiform and strictly ascending, 2–4 cm. long and about 1 mm. broad, usually strongly revolute, glabrous or essentially so. Inflorescences subterminal, corymbosely clustered at the uppermost nodes, several-flowered; peduncles 1.0–1.5 cm. long; pedicels slender, about 1 cm. long. Flowers small; calyx lobes lance-trigonal, about 1 mm. long, scatteringly pilosulose to nearly glabrous; corolla reflexed-rotate, white or faintly suffused with rose or yellowish green, the lobes 2–3 mm. long; gynostegium narrowly stipitate, greenish white, the column cylindrical, about 1 mm. long and broad, the hoods cucullate, broadly oval, about 1.5 mm. long, the basal horn narrowly acicular,

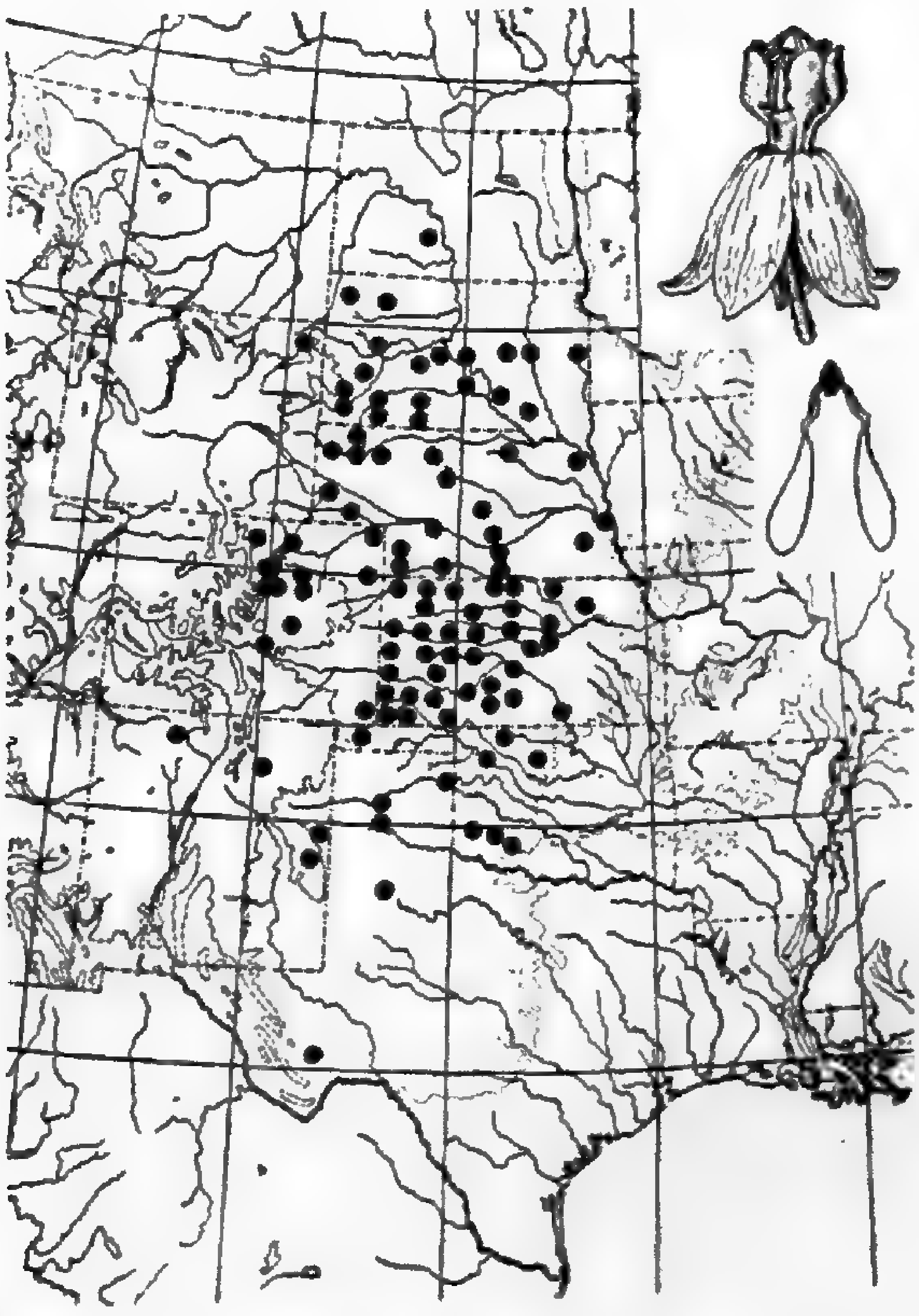

Fig. 20. *Asclepias pumila* (A. Gray) Vail

almost twice longer than the hood and gradually arching over the anther head, the anther head cylindric, about 1.25 mm. long and 1 mm. broad. Follicles erect on erect pedicels, narrowly fusiform, 4–8 cm. long, about 6 mm. broad; seeds broadly oval, 4–6 mm. long, the white coma about 2.5 cm. long.

Great Plains, from North Dakota to Texas and westward to Wyoming and New Mexico; poisonous to stock. Flowering from June to September.

UNITED STATES:

COLORADO: Adams, Arapahoe, Baca, Bouider, Denver, El Paso, Fremont, Jefferson, Larimer, Sedgwick, Weld, and Yuma counties.

KANSAS: Barton, Cheyenne, Cloud, Decatur, Dodge, Edwards, Ellis, Ellsworth, Finney, Ford, Gove, Graham, Grant, Gray, Greeley, Hamilton, Haskell, Hodgeman, Kiowa, Logan, Marion, Meade, Morton, Ness, Osborne, Pawnee, Phillips, Pratt, Rawlins, Republic, Riley, Rook, Russell, Saline, Scott, Sheridan, Smith, Stafford, Stanton, Stevens, Thomas, Trego, Wallace, and Wichita counties.

NEBRASKA: Banner, Box Butte, Buffalo, Chase, Cherry, Cheyenne, Custer, Dawes, Dixon, Dundy, Franklin, Holts, Kearney, Lancaster, Lincoln, Red Willow, Sarpy, Sheridan, Sioux, and Thomas counties.

NEW MEXICO: Curry, Mora, Rio Arriba, and Roosevelt counties.

NORTH DAKOTA: Morton County.

OKLAHOMA: Cimarron, Comanche, Garfield, Greer, Kiowa, Woods, and Woodward counties.

SOUTH DAKOTA: Beadle, Brookings, Brule, Custer, Douglas, Fall River, Haakon, Hand, Harding, Hughes, Lyman, Meade, Pennington, Perkins, Shannon, Stanley, Todd, Washabaugh, and Washington counties.

TEXAS: Brewster, Hemphill, Lubbock, Potter, and Randall counties.

WYOMING: Crook County.

Slight development of obtuse marginal lobes to the hoods may be indicative of occasional hybridization with *A. verticillata* in the east.

15. **ASCLEPIAS LEPTOPUS** I. M. Johnston, in Proc. Cal. Acad. Sci. Ser. IV, 12:1127. 1924. [T.: *Johnston 4377*, CAS!]

Asclepias suffrutex Standl. in Field Mus. Publ. Bot. 22:45. 1940. [T.: *Gentry 2388*, MO!]

Suffruticose perennials or subshrubs. Stems very slender, 3–4 dm. tall, branching repeatedly at least toward the persistent woody base, glabrous. Leaves opposite, sessile, relatively distant and caducous soon after flowering, filiform, lax, 4–6 cm. long, about 1 mm. broad, glabrous, revolute. Inflorescences subterminal from few of the uppermost nodes, few-flowered; peduncle 0.5–1.2 cm. long; pedicels slender, 1–2 cm. long. Flowers rather small; calyx lobes narrowly trigonal, 1.5–2.5 mm. long, glabrous; corolla reflexed-rotate, white, the lobes 4.5–7.0 mm. long; gynostegium narrowly stipitate, white, the column cylindrical, about 1 mm. long and broad, the hoods cucullate-elliptic, 3–5 mm. long, the basal horn narrowly acicular, about as long as the hood and arching over the anther head, the anther head cylindric, about 2.0–2.5 mm. long and broad. Follicles pendulous or subpendulous, narrowly fusiform, 4–6 cm. long, smooth, glabrous; seeds broadly oval, about 2.5 mm. long, the pale tawny coma about 1 cm. long.

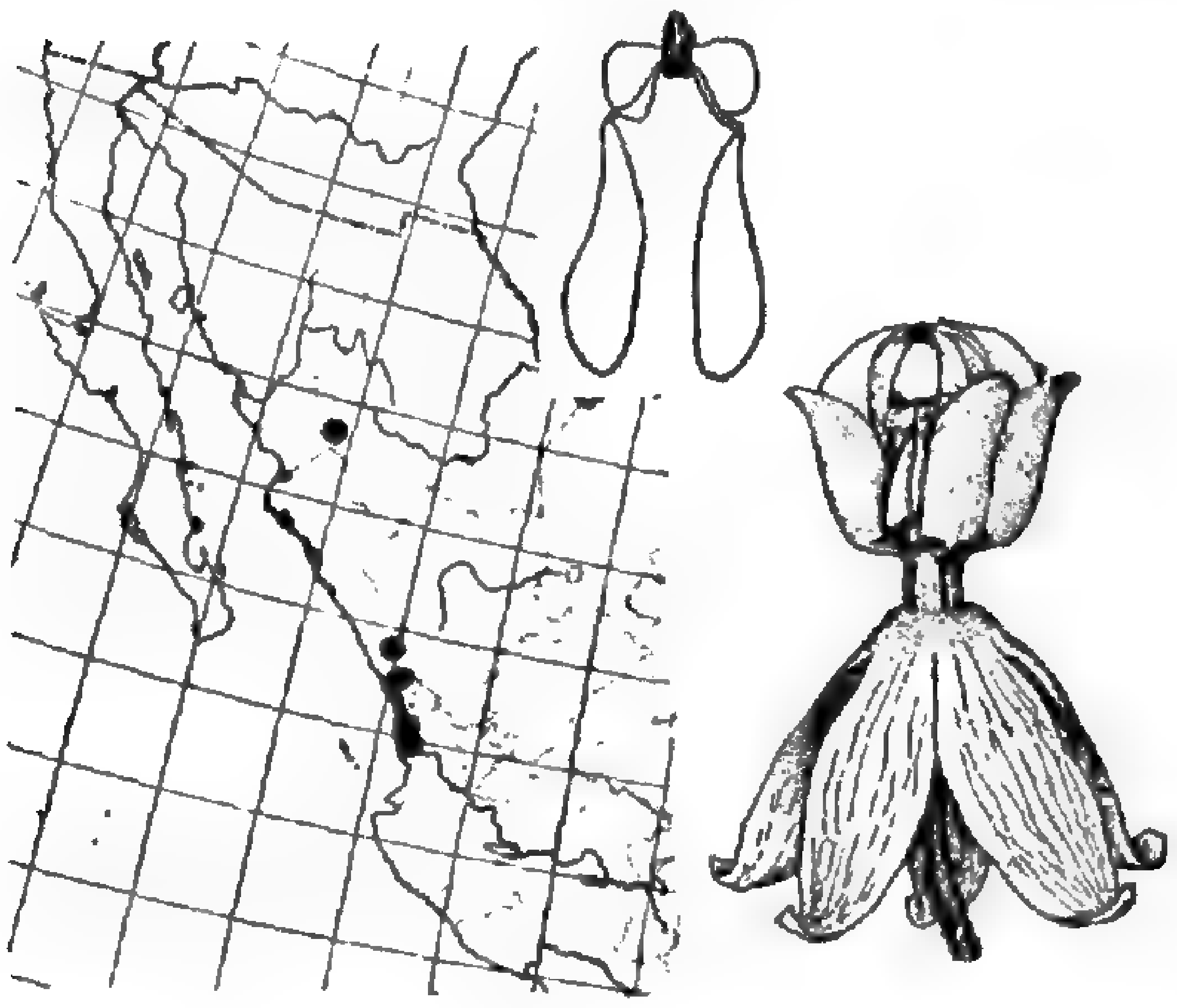

Fig. 21. *Asclepias leptopus* I. M. Johnston

Crevices of rock and tufa and in canyons; northwestern Mexico. Flowering from July to December.

MEXICO: CHIHUAHUA: Río Mayo. SINALOA: Culiacan, Cerro Colorado. SONORA: San Bernardo, San Carlos Bay, Guaymas, Hermosillo.

The twiggy, glaucous, *Ephedra*-like plants of this species closely resemble certain other milkweeds native to this region, such as *A. masonii*, *A. subaphylla*, *A. albicans*, and *A. subulata*, when out of flower.

16. ASCLEPIAS GENTRYI Standl. in Field Mus. Publ. Bot. 22:45. 1940. [T.: *Gentry 2330*, MO!]

Herbaceous perennials from rather superficial rootstalks. Stems usually simple, 1–2 dm. tall, minutely puberulent in decurrent lines from the nodes. Leaves opposite, shortly petiolate, persistent, linear to linear-lanceolate, acuminate, the base acute to obtuse, 3–8 cm. long, 2–5 mm. broad, membranaceous, inconspicuously pilosulose to glabrate, membranaceous, usually somewhat revolute; petioles 1–3 mm. long. Inflorescences terminal and subterminal from the uppermost nodes, few- to several-flowered; peduncles 2–3 cm. long; pedicels 1–5 cm. long, very slender. Flowers moderately large; calyx lobes lance-trigonal, 2–3 mm. long, glabrous; corolla reflexed-rotate, bright red to pinkish, the lobes 6–7 mm. long; gynostegium narrowly stipitate, yellow or slightly pinkish, the column cylindrical, 1.0–1.5 mm. long, 0.5–1.0 mm. broad, the hoods oblong-elliptic, 3–4 mm. long, the horn acicular, adnate to near the tip of the hood and slightly longer than it, gradually arching over the anther head, the anther head about 2 mm. long and broad. Follicles unknown.

Barren slopes and hillsides, amongst short grass; western Mexico from Chihuahua to Nayarit. Flowering in July and August.

MEXICO: CHIHUAHUA: Río Mayo. NAYARIT: Punta Mita, Tepic. SINALOA: Rosario, Colomos.

This is a very peculiar species of uncertain affinity in the absence of fruit. The strongly adnate horns are unusual for the INCARNATAE, but most unusual for the entire genus are the broadly triangular translator arms which suggest those of the genus *Oxypetalum*.

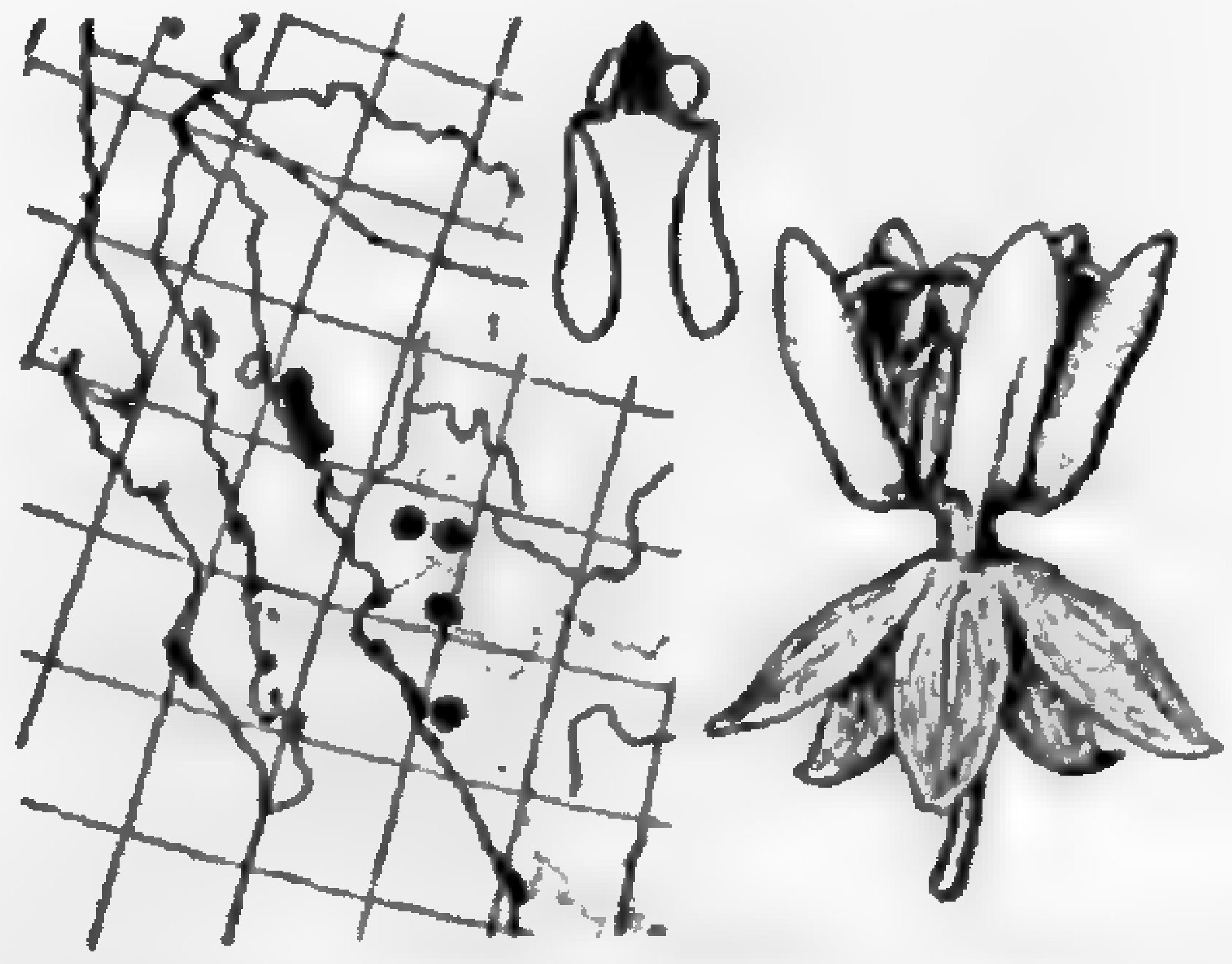

Fig. 22. *Asclepias gentryi* Standl.

Series 2. TUBEROSAE

KEY TO THE SPECIES

a. Plants conspicuously hirsutulous or hispid generally; leaves irregularly approximate; corolla orange, rarely yellow or red. Southern Ontario; New Hampshire to Florida and westward to South Dakota, Utah, and Arizona; Tamaulipas to Chihuahua..........................17. *A. tuberosa*
aa. Plants essentially glabrous; leaves opposite; corolla red or purplish.
  b. Hoods acute, about three times as long as the anther head; leaves broadly ovate to lanceolate. New Jersey to Georgia and westward to southeastern Texas...............18. *A. rubra*
  bb. Hoods broadly rounded, about twice as long as the anther head; leaves linear-lanceolate. New Jersey to Florida and westward to southeastern Texas..............................19. *A. lanceolata*

From the standpoint of floral structure these three species probably are closely related. Since their vegetative aspect is so different, however, perhaps it might be better to erect at least a separate subseries for *A. tuberosa.* So few species are involved and so little is actually known of the phylogeny of *Asclepias,* particularly in the role of parallelism of development of the gynostegium, on the other hand, that little would be gained.

17. **ASCLEPIAS TUBEROSA** L. Sp. Pl. 217. 1753. [T.: Linn. Herb. London, no. *310.41*, photo!]

Herbaceous perennials from a deep, woody rootstalk Stems usually stout and clustered from the crown, usually branching only at the inflorescence, 2–9 dm. tall, conspicuously hirsutulose or hispid generally. Leaves irregularly approximate, usually crowded, rather shortly petiolate, extremely variable, very narrowly lanceolate to very broadly oblanceolate, apex acuminate to rounded, base cuneate to broadly cordate, 3–11 cm. long, 0.3–3.0 cm. broad, firmly membranaceous and occasionally irregularly crisped-revolute, more or less conspicuously hirsutulose particularly beneath; petioles 1–5 mm. long. Inflorescence of 1 to several terminal and subterminal helicoid branches bearing few to numerous umbelliform cymes at the nodes of the more or less reduced and usually opposite leaves, the cymes several- to many-flowered. Flowers moderately large; calyx lobes lance-trigonal, 2–3 mm. long, minutely hirsutulous; corolla reflexed-rotate, usually orange or occasionally reddish or yellow or red, the lobes 7–8 mm. long; gynostegium usually orange, rarely yellow, the column narrowly obconic, about 2 mm. long and 1.5 mm. broad, the hoods cucullate, lanceolate, 4–5 mm. long, the horn basal, narrowly acicular, slightly longer than the hoods, gradually arching over the anther head, the anther head cylindrical, about 2 mm. long and broad. Follicles erect on deflexed pedicels, narrowly fusiform, 8–15 cm. long, 1.0–1.5 cm. broad, smooth, pilosulose; seeds broadly oval, 5–7 mm. long, the white coma 3–4 cm. long.

KEY TO THE SUBSPECIES

Leaves typically obovate to oblanceolate and cuneate at the base, varying to oblong or elliptic, the margins usually flat. New Hampshire to northern Florida (there merging with ssp. *rolfsii*) westward to the Alleghenies (there merging with ssp. *interior*)....17a. ***A. tuberosa tuberosa***
Leaves typically hastate, the margins usually crispate-revolute. Florida to Georgia (there merging with ssp. *tuberosa*) and westward along the Gulf plain to Alabama (there merging with sspp. *tuberosa* and *interior*)..17b. ***A. tuberosa rolfsii***

Leaves lanceolate to ovate, varying to oblong or elliptic, the margins usually flat.
  Leaves typically deeply cordate. Ozark upland eastward to the Alleghenies (there merging with ssp. *tuberosa*), southward to the Gulf plain (there merging with ssp. *rolfsii*), and in an arc westward and northward from Texas to northern Michigan (there merging with ssp. *terminalis*) ....17c. *A. tuberosa interior*
  Leaves typically obtuse to truncate at the base, varying to slightly cordate. Western periphery of the species distribution from Tamaulipas northwestward to southern Utah, and eastward to Colorado, South Dakota, southern Minnesota, Wisconsin, and northern Michigan (merging in an arc generally eastward and southward with ssp. *interior*) ....17d. *A. tuberosa terminalis*

The complicated population patterns of *A. tuberosa* have been the subject of rather detailed biometric studies (Woodson, in Ann. Missouri Bot. Gard. 34:353. 1947; Proc. Nat. Acad. Sci. 39:74. 1953) which are being continued at present. Although the existence of the subspecies is readily demonstrable statistically and easily observed in relatively homozygous individuals, a large part of the species population as a whole consists of the very broad commissures where introgression is extremely active. Here exact assignment of individual plants to any given subspecies frequently is quite impossible.

Since these commissures evidently are genoclines, I have sought to cut the Gordian knot in the naming of their specimens by labelling them "*Asclepias t.* cl.

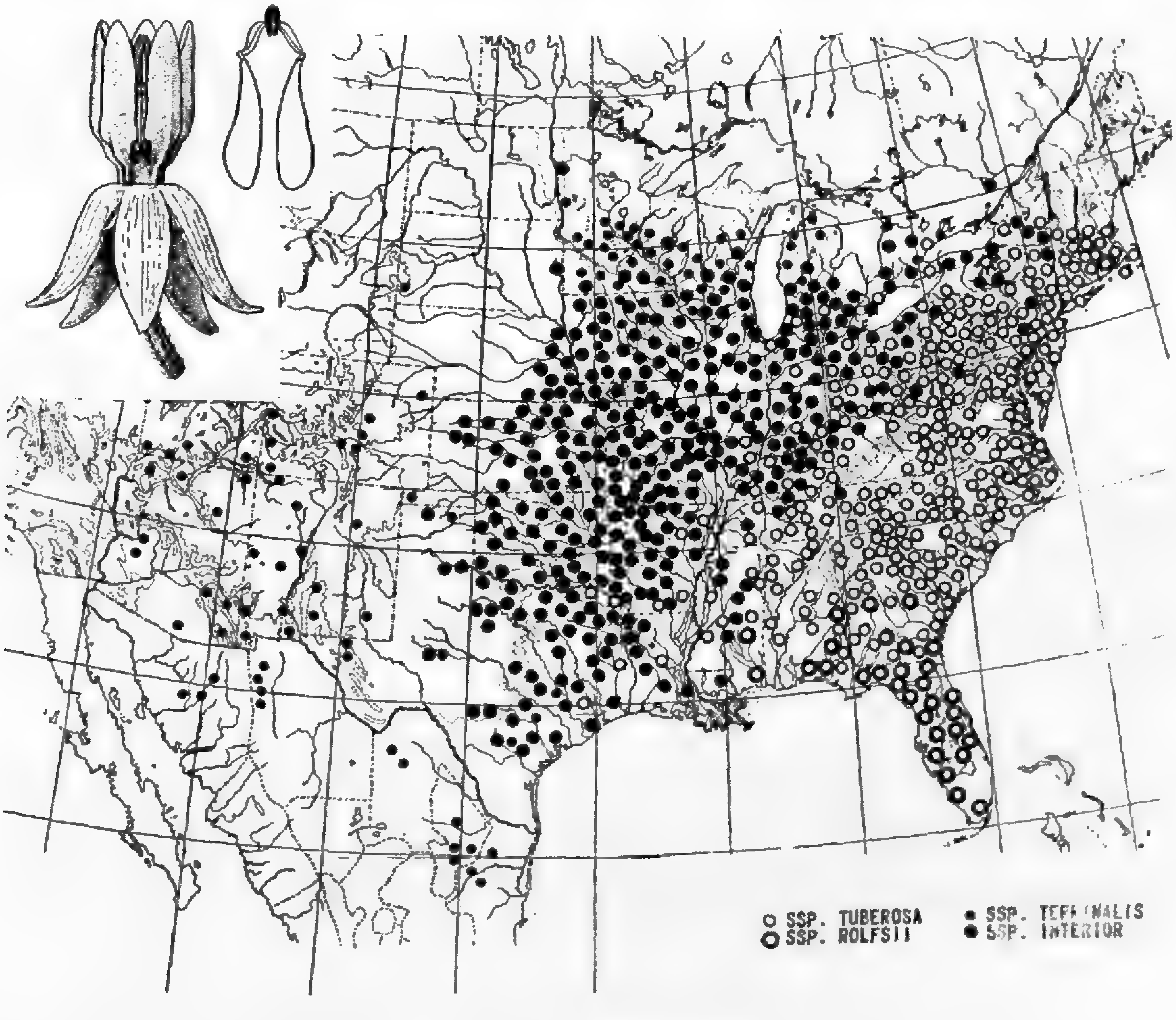

Fig. 23. *Asclepias tuberosa* L.

interior-tuberosa", "*Asclepias t.* cl. *rolfsii-tuberosa*", or whatever the case appears to be. In the geographic citations which follow, however, this device is not used as being too ambiguous. The result is a frequently too arbitrary assignment of county records to the various subspecies, which may leave the reader with a scarcely more fortunate mis-impression of genetic stability within the populations. It is, nevertheless, more in harmony with current taxonomic practice.

17a. ASCLEPIAS TUBEROSA ssp. TUBEROSA

Asclepias decumbens L. Sp. Pl. 216. 1753, ex char.
Asclepias floridana Lam. Encycl. 1:284. 1783. [T.: Herb. Lam., Paris, photo!]
Asclepias lutea Raf. Med. Repos. N. Y. 5:361. 1808, ex char.
Asclepias tuberosa β *decumbens* (L.) Pursh, Fl. Amer. Sept. 1:184. 1814.

Dry fields, hillsides, thickets, and open woods; sand dunes. Southern Ontario; New Hampshire to northern Florida and westward to Michigan and Tennessee (merging with ssp. *rolfsii* in the south and with ssp. *interior* in the west). Flowering from April to September.

CANADA: ONTARIO: Carleton and Welland counties.

UNITED STATES:

ALABAMA: Barbour, Cullman, Elmore, Franklin, Houston, Jackson, Lee, Mobile, and Montgomery counties.

CONNECTICUT: Fairfield, Hartford, Middlesex, New Haven, New London, Tolland, and Windham counties.

DELAWARE: Kent, New Castle, and Sussex counties.

FLORIDA: Duval, Holmes, and Nassau counties.

GEORGIA: Bibb, Charlton, Chatham, Clarke, Dade, De Kalb, Dougherty, Effingham, Fannin, Floyd, Forsyth, Fulton, Gwinnett, Hall, Heard, Jefferson, Jenkins, Lamar, Lincoln, Long, Lowndes, McDuffie, McIntosh, Meriwether, Muscogee, Oglethorpe, Pickens, Quitman, Rabun, Richmond, Stephens, Terrell, Union, Walker, White, and Wilkes counties.

ILLINOIS: Williamson County.

KENTUCKY: Calloway, Marshall, McCreary, and Washington counties.

MARYLAND: Allegany, Caroline, Cecil, Garrett, Harford, Montgomery, Prince Georges, Queen Anne, Talbot, and Wicomico counties.

MASSACHUSETTS: Barnstable, Berkshire, Bristol, Dukes, Essex, Franklin, Hampden, Hampshire, Middlesex, Nantucket, Norfolk, Plymouth, and Worcester counties.

MISSISSIPPI: Harrison, Jackson, Lauderdale, and Oktibbeha counties.

NEW HAMPSHIRE: Cheshire and Hillsborough counties.

NEW JERSEY: Atlantic, Bergen, Burlington, Camden, Cape May, Cumberland, Essex, Gloucester, Hunterdon, Mercer, Middlesex, Monmouth, Morris, Ocean, Passaic, Salem, Somerset, Sussex, and Warren counties.

NEW YORK: Albany, Bronx, Cayuga, Columbia, Dutchess, Fulton, Kings, Nassau, New York, Oneida, Ontario, Orange, Queens, Rensselaer, Richmond, Rockland, Saratoga, Seneca, Suffolk, Sullivan, Warren, Washington, and Westchester counties.

NORTH CAROLINA: Alexander, Bertie, Buncombe, Cabarrus, Catawba, Cherokee, Chowan, Cleveland, Cumberland, Currituck, Dare, Davidson, Durham, Forsyth, Gates, Granville, Graham, Greene, Guilford, Harnett, Haywood, Henderson, Jackson, McDowell, Macon, Madison, Martin, Onslow, Orange, Polk, Randolph, Rowan, Sampson, Stanly, Surry, Swain, Union, Wake, Washington, Wilkes, and Wilson counties.

OHIO: Erie, Jackson, and Richland counties.

PENNSYLVANIA: Adams, Allegheny, Armstrong, Beaver, Bedford, Berks, Bradford, Bucks, Butler, Center, Chester, Cumberland, Delaware, Huntingdon, Juniata, Lackawanna, Lancaster, Lebanon, Lehigh, Luzerne, Mifflin, Montgomery, Montour, Perry, Philadelphia, Schuylkill, Snyder, Susquehanna, Warren, Washington, Westmoreland, Wyoming, and York counties.

RHODE ISLAND: Providence and Washington counties.

SOUTH CAROLINA: Abbeville, Aiken, Anderson, Beaufort, Berkeley, Charleston, Darlington, Florence, Horry, Lancaster, Lexington, Oconee, Pickens, and Williamsburg counties.

TENNESSEE: Anderson, Bledsoe, Blount, Campbell, Cocke, Davidson, Franklin, Grainger, Knox, Monroe, McNary, Sevier, and Union counties.

VERMONT: Bennington and Windham counties.

VIRGINIA: Allegheny, Bath, Bedford, Cumberland, Dinwiddie, Fauquier, Frederick, Giles, Gloucester, Greensville, Henrico, James City, Nansemond, Norfolk, Northumberland, Patrick, Prince William, Princess Anne, Roanoke, Rockbridge, Rockingham, Southampton, Sussex, Tazewell, and Warren counties.

WEST VIRGINIA: Berkeley, Cabell, Gilmer, Grant, Hardy, Harrison, Jefferson, Kanawha, Marion, Mercer, Mineral, Monongalia, Monroe, Morgan, Ohio, Pendleton, Preston, Raleigh, Randolph, Ritchie, Tyler, Upshur, Wetzel, and Wood counties.

17b. ASCLEPIAS TUBEROSA ssp. ROLFSII (Britton) Woodson, in Ann. Missouri Bot. Gard. 31:368. 1944.

Asclepias Rolfsii Britton, in Small, Fl. Southeast. U. S. 943, 1336. 1903. [T.:*Britton s. n.*, NY!]
Asclepias tuberosa var. *Rolfsii* (Britton) Shinners, in Field & Lab. 17:89. 1949.

Sandy and rocky soil, fields, pine barrens, and flatwoods. Florida and southern Georgia to South Carolina and Mississippi (merging northward with ssp. *tuberosa* and northwestward with ssp. *interior*). Flowering from February to August.

UNITED STATES:

ALABAMA: Houston, Macon, and Russell counties.

FLORIDA: Alachua, Baker, Bradford, Brevard, Citrus, Clay, Collier, Columbia, Dade, Dixie, Duval, Gadsden, Gilchrist, Highlands, Hillsborough, Holmes, Jefferson, Lee, Leon, Levy, Liberty, Manatee, Marion, Okaloosa, Okeechobee, Orange, Osceola, Pinellas, Polk, Putnam, Sumter, Suwanee, and Volusia counties.

GEORGIA: Bulloch, Charlton, Dougherty, Emanuel, Laurens, Lowndes, McIntosh, and Macon counties.

MISSISSIPPI: Scott County.

17c. ASCLEPIAS TUBEROSA ssp. INTERIOR Woodson, in Ann. Missouri Bot. Gard. 31:368. 1944. [T.: *A. Hayden 3195*, MO!]

Asclepias tuberosa var. *flexuosa* James, in Bot. Gaz. 13:271. 1888, ex char. [T.: *Miss Mohr s. n.*]
Asclepias tuberosa f. *lutea* Clute, in Amer. Bot. 18:73. 1912, ex char.
Asclepias tuberosa f. *flavescens* Farwell, in Papers Mich. Acad. Sci. 2:36. 1923, ex char. [T.: *Farwell 5875*]
Asclepias tuberosa f. *bicolor* Standl. in Rhodora 32:33. 1930. [T.: *Standley 57304*, F!]
Asclepias tuberosa var. *interior* (Woodson) Shinners, in Field & Lab. 17:89. 1949.

Prairies, glades, fields, thickets, and open woods. Southern Ontario; western New York southeastward to Mississippi and westward to Minnesota, Nebraska, Kansas, Oklahoma, and Texas (merging eastward with ssp. *tuberosa*, southward with ssp. *rolfsii*, and westward with ssp. *terminalis*). Flowering from May to September.

Canada: ontario: Bruce, Carleton, Essex, Hastings, Huron, Kent, Lambton, Middlesex, Ontario, Simcoe, Wentworth, and York counties.

United States:

arkansas: Baxter, Benton, Boone, Clark, Cleburne, Cleveland, Craighead, Drew, Faulkner, Garland, Greene, Hempstead, Hot Springs, Jefferson, Lawrence, Little River, Logan, Lonoke, Miller, Montgomery, Nevada, Phillips, Polk, Pope, Pulaski, Prairie, Saline, Searcy, Sevier, Sharp, Washington, and Yell counties.

california: Colusa County (Princeton, introduced).

illinois: Adams, Calhoun, Champaign, Clay, Cook, Du Page, Effingham, Jefferson, Jackson, Kankakee, Lake, La Salle, Logan, McLean, Macon, Macoupin, Madison, Mason, Massac, Ogle, Peoria, Putnam, Rock Island, Stark, Vermilion, Winnebago, and Woodford counties.

indiana: Allen, Benton, Brown, Cass, Clark, Clinton, Crawford, Daviess, De Kalb, Elkhart, Fountain, Fulton, Greene, Jasper, Jennings, Knox, Kosciusko, Lagrange, Lake, La Porte, Lawrence, Marshall, Martin, Monroe, Newton, Noble, Owen, Pike, Porter, Pulaski, Putnam, St. Joseph, Stark, Steuben, Sullivan, Tippecanoe, Tipton, Union, Vermillion, Vigo, Wabash, Washington, Warren, Wells, White, and Whitley counties.

iowa: Adair, Allamakee, Appanose, Benton, Carroll, Cerro Gordo, Chickasaw, Clay, Clinton, Crawford, Decatur, Dickinson, Douglas, Emmet, Fayette, Greene, Hamilton, Harrison, Henry, Humboldt, Johnson, Lee, Madison, Mitchell, Muscatine, Palo Alto, Pocahontas, Poweshiek, Ringgold, Shelby, Sioux, Story, Union, Van Buren, Webster, Winneshiek, and Wright counties.

kansas: Allen, Anderson, Atchison, Barton, Brown, Butler, Chautauqua, Cherokee, Cloud, Crawford, Custer, Ellis, Ellsworth, Franklin, Geary, Greenwood, Harvey, Jackson, Jefferson, Johnson, Labette, Leavenworth, Lincoln, Lyon, Marion, Marshall, Miami, Mitchell, Montgomery, Morris, Nemaha, Neosho, Osage, Osborne, Pottawatomie, Rice, Riley, Rooks, Russell, Saline, Sedgwick, Shawnee, Sumner, Trego, Wabaunsee, Washington, Whitford, Woodson, and Wyandotte counties.

kentucky: Barren, Breckenridge, Caldwell, Graves, Logan, McCreary, Ohio, Taylor, and Warren counties.

louisiana: Ascension, Bienville, Caddo, De Soto, Natchitoches, Rapides, St. Martins, and St. Tammany parishes.

michigan: Allegan, Berrien, Calhoun, Crawford, Eaton, Emmet, Grand Traverse, Hillsdale, Ingham, Ionia, Jackson, Kalamazoo, Kent, Lake, Lenawee, Livingston, Mason, Muskegon, St. Clair, St. Joseph, Van Buren, Wayne, and Washtenaw counties.

minnesota: Benton, Brown, Chippewa, Chisago, Faribault, Goodhue, Hennepin, Houston, Isanti, Jackson, Kandiyohi, Nicollet, Olmstead, Ottertail, Polk, Ramsey, Rice, Scott, Sherburne, Stearns, Todd, Wabasha, Waseca, Winona, and Wright counties.

mississippi: Choctaw, Grenada, Oktibbeha, Panola, Rankin, and Scott counties.

missouri: Barry, Barton, Boone, Callaway, Cass, Chariton, Cooper, Daviess, Dent, Franklin, Greene, Grundy, Iron, Jasper, Jefferson, Johnson, Laclede, Lafayette, Lawrence, Lewis, Lincoln, McDonald, Madison, Marion, Morgan, Nodaway, Phelps, Pike, St. Clair, Ste. Genevieve, St. Louis, Stone, Taney, Wayne, and Wright counties.

nebraska: Butler, Cass, Dodge, Douglas, Gage, Jefferson, Lancaster, Nemaha, Nuckolls, Otoe, Richardson, Saline, Sarpy, Saunders, Washington, and Webster counties.

new york: Cayuga, Chemung, Herkimer, Monroe, Niagara, Schenectady, Seneca, Tioga, Tompkins, and Wayne counties.

ohio: Adams, Ashtabula, Auglaize, Brown, Butler, Carroll, Champaign, Cuyahoga, Defiance, Erie, Fairfield, Fayette, Greene, Lake, Licking, Logan, Lorain, Lucas, Madison, Miami, Montgomery, Perry, Portage, Richland, Ross, Stark, Summit, Williams, and Wyandot counties.

oklahoma: Beckham, Caddo, Canadian, Carter, Cherokee, Choctaw, Cleveland, Coal, Comanche, Craig, Creek, Custer, Garfield, Grady, Greer, Haskell, Hughes, Jackson, Johnston, Kay, Kingfisher, Kiowa, Le Flore, Lincoln, Logan, Love, McLain, McCurtain, McIntosh, Mayes, Murray, Muskogee, Noble, Nowata, Oklahoma, Pawnee, Payne, Pittsburg, Pottawatomie, Pushmataha, Roger Mills, Rogers, Seminole, Tulsa, Wagoner, Washita, and Woods counties.

PENNSYLVANIA: Bradford, Lackawanna, Philadelphia, Snyder, Venango, and Warren counties.

SOUTH DAKOTA: Brookings, Lincoln, and Union counties.

TENNESSEE: Davidson County.

TEXAS: Anderson, Angelina, Bastrop, Bexar, Bowie, Brown, Brazos, Callahan, Cass, Cherokee, Childress, Comanche, Denton, De Witt, Eastland, Ellis, Erath, Fayette, Galveston, Goliad, Gonzales, Grayson, Gregg, Hall, Harris, Harrison, Henderson, Hill, Hood, Hopkins, Houston, Hunt, Jasper, Jefferson, Kerr, Lamar, Leon, Madison, Montague, Montgomery, Parker, Roberts, Tarrant, Taylor, Travis, Trinity, Upshur, Victoria, Walker, Washington, Wichita, Williamson, Wilson, Wise, and Wood counties.

WEST VIRGINIA: Hampshire and Wirt counties.

WISCONSIN: Adams, Barron, Brown, Burnett, Buffalo, Clark, Crawford, Dane, Dunn, Eau Claire, Grant, Green, Green Lake, Jackson, Juneau, La Crosse, Lafayette, Marinette, Milwaukee, Oconto, Portage, Racine, Rock, Shawano, Vernon, Walworth, Waukesha, Waupaca, Waushara, Winnebago, and Wood counties.

17d. ASCLEPIAS TUBEROSA ssp. TERMINALIS Woodson, in Proc. Nat. Acad. Sci. 39:79. 1953. [T.: *L. S. Ehlers 13954*, MO!]

Prairies, open oak and pine woods, canyons, stream sides and arroyos. Western Texas to Arizona and southern Utah and northeastward to Colorado, South Dakota, Minnesota, and northern Wisconsin and Michigan (merging generally eastward with ssp. *interior*); northern Mexico. Flowering from June to September.

UNITED STATES:

ARIZONA: Apache, Cochise, Coconino, Gila, Graham, Maricopa, Mohave, Navajo, Pima, and Yavapai counties.

COLORADO: Denver, El Paso, Fremont, La Plata, Mesa, Montrose, Pueblo, and Yuma counties.

MICHIGAN: Cheboygan, Emmet, and Grand Traverse counties.

MINNESOTA: Benton, Mille Lacs, Ramsey, Sherburne, Stearns, and Wabasha counties.

NEW MEXICO: Bernalillo, Catron, Dona Ana, Eddy, Grant, Hidalgo, Lincoln, Otero, Sandoval, San Juan, San Miguel, Sierra, Socorro, and Union counties.

OKLAHOMA: Cimarron County.

SOUTH DAKOTA: Fall River County.

TEXAS: Culberson, Hutchinson, Jeff Davis, Parker, Taylor, and Tom Green counties.

UTAH: Garfield, Kane, San Juan, and Washington counties.

WISCONSIN: Burnett, Eau Claire, Marinette, Pierce, and Polk counties.

MEXICO: CHIHUAHUA: Colonia García, Colonia Juárez, Tosanachic, Chuichupa, Chuchuichupa. COAHUILA: Villa Acuña, Monclova. NUEVO LEON: Dulces Nombres, Villa Santiago, Montemorelos, Monterrey, Galeana, Río Ramos. SONORA: Sierra de El Tigre, Bavispe, Sierra del Pajarito. TAMAULIPAS: San Lucas, Jaumave, San José.

The naming of ssp. *terminalis* is the result of afterthought since the publication of my first paper of leaf variation in *A. tuberosa* (Ann. Missouri Bot. Gard. 34:353–432. 1947). In that paper, phenocontour maps revealed a striking series of isophenes radiating from the Ozark upland, with respect to the leaf base of *A. t. interior*. In the center of the distribution leaves of that subspecies are deeply cordate; but radiating in remarkably concentric waves in broad arcs roughly westward from Lake Erie to north-central Mexico, the leaf bases become less and less deeply cordate, to truncate and finally obtuse. No taxonomic designation was given the peripheral population at that time, however.

Now it seems best to do so, particularly since a "crest of variability" midway between the distributions of the two extremes shows plainly that the intergradation observed is the result of introgression and thus a genocline and not a simple geocline or ecocline.

18. Asclepias rubra L. Sp. Pl. 217. 1753. [T.: Linn. Herb. London, no. *310.39*, photo!]

Asclepias cordata Walt. Fl. Carol. 105. 1788, ex char.
Asclepias laurifolia Michx. Fl. Bor. Amer. 1:117. 1803, ex char.
Asclepias acuminata Pursh, Fl. Amer. Sept. 1:182. 1816, ex char.
Asclepias periplocaefolia Nutt. Gen. North Amer. Pl. 1:167. 1818, ex char.
Asclepias rubra var. (Michx.) *laurifolia* Harper, in Bull. Torrey Bot. Club 30:339. 1903.

Herbaceous perennials. Stems rather slender, 4–10 dm. tall, simple, glabrous or very inconspicuously pilosulose in decurrent lines from the nodes. Leaves opposite, sessile or subsessile, broadly ovate to narrowly lanceolate, apex acute to acuminate, base rounded to somewhat cordate, 5–16 cm. long, 1.0–6.5 cm. broad, firmly membranaceous, glabrous, dark green above, glaucous beneath. Inflorescences terminal and lateral from the uppermost nodes, commonly paired when terminal, several- to many-flowered; peduncles 3–10 cm. long; pedicels 1.0–1.5 cm. long. Flowers moderately large; calyx lobes lance-trigonal, about 3 mm. long, glabrous; corolla reflexed-rotate, dull red to purplish or lavender, the lobes 8–9 mm. long;

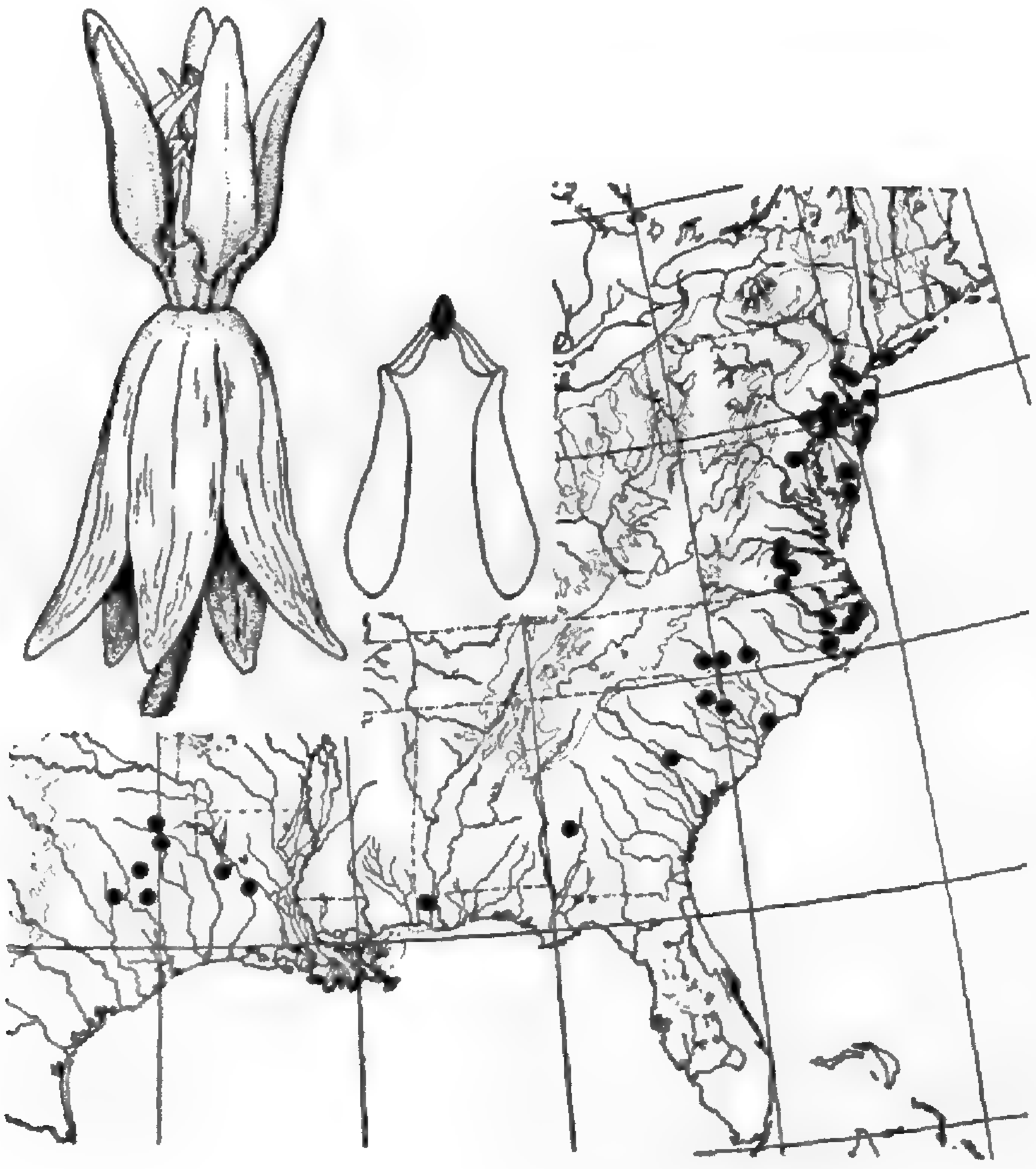

Fig. 24. *Asclepias rubra* L.

gynostegium stipitate, usually pinkish cream or purplish, the column cylindrical, about 2 mm. long and broad, the hoods lanceolate, acute, 6–7 mm. long, the basal horn narrowly acicular, somewhat shorter than the hoods, gradually arching over the anther head, the anther head narrowly conic, about 3 mm. long and broad, with entire or very inconspicuously notched wings. Follicles erect on deflexed pedicels, rather narrowly fusiform, about 8–12 cm. long and 1.5 cm. thick, smooth, glabrous; seeds broadly oval, about 7 mm. long, the white coma about 4 cm. long.

Bogs, marshes, wet meadows, and low pine barrens. New Jersey to southern Georgia; southern Alabama, Louisiana, and southeastern Texas. Flowering from May to August.

UNITED STATES:
ALABAMA: Mobile County.
DELAWARE: New Castle and Sussex counties.
GEORGIA: Sumter County.
LOUISIANA: Natchitoches and Rapides parishes.
MARYLAND: Prince Georges and Worcester counties.
NEW JERSEY: Atlantic, Burlington, Cape May, Gloucester, Hunterdon, Middlesex, and Ocean counties.
TEXAS: Anderson, Houston, Robertson, Smith, and Wood counties.

19. ASCLEPIAS LANCEOLATA Walt. Fl. Carol. 105. 1788, ex char.

Asclepias serpentaria Raf., Fl. Ludov. 52. 1817, ex char.
Asclepias paupercula Michx. Fl. Bor.-Amer. 1:118. 1803, ex char.
Asclepias lanceolata var. *paupercula* (Michx.) Fernald, in Rhodora 37:438. 1935.
Asclepias lanceolata var. *paupercula* f. *flaviflora* Fernald, loc. cit. 45:458. 1943. [T.: *Fernald & Long 14,390*, GH!]

Herbaceous perennials from rather tuberous rootstalks. Stems relatively slender, simple, 5–12 dm. tall, glabrous or essentially so. Leaves opposite, linear-lanceolate,

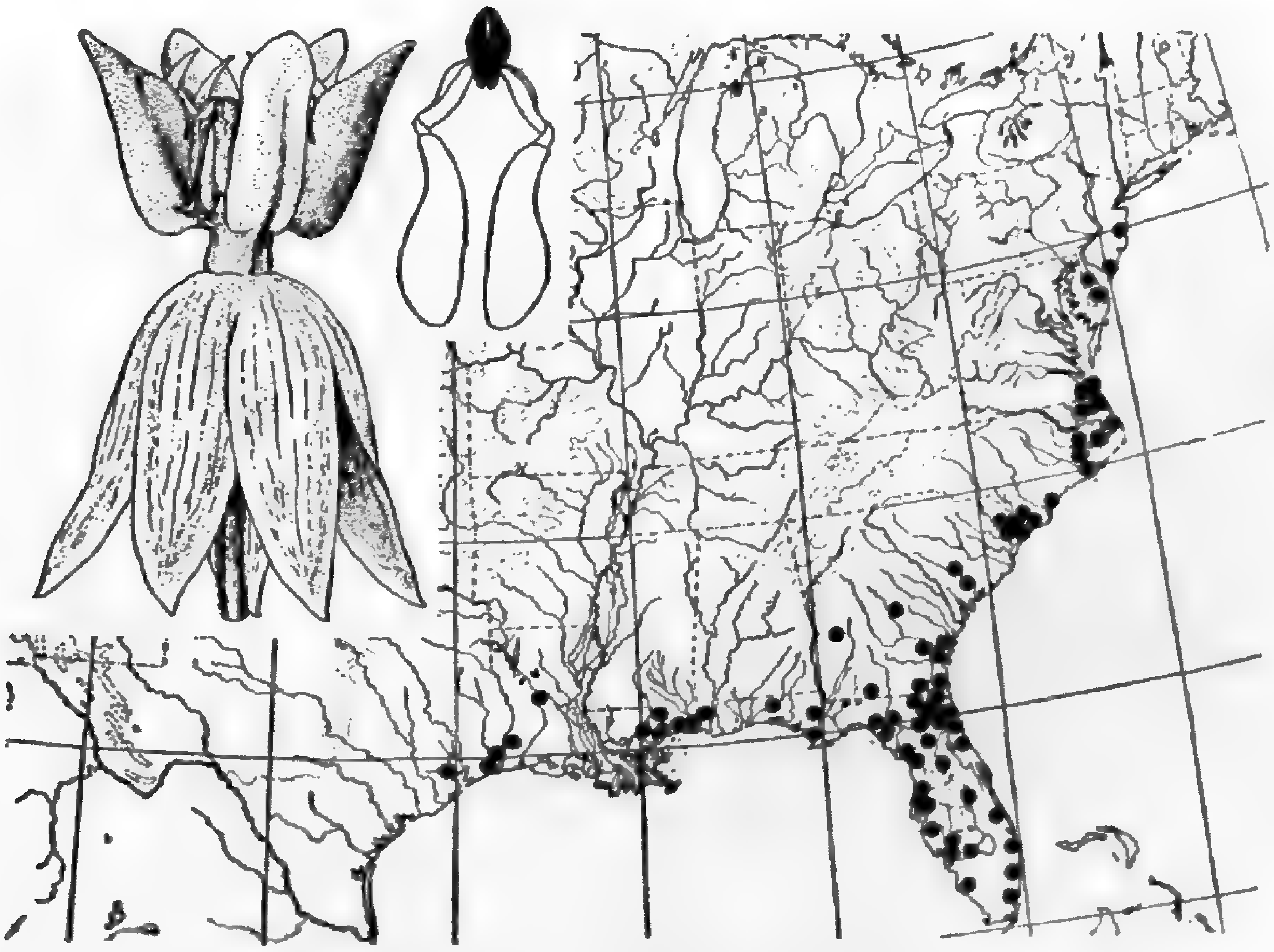

Fig. 25. *Asclepias lanceolata* Walt.

narrowly acuminate, acute to obtuse at the base, 7–25 cm. long, 0.5–1.7 cm. broad, firmly membranaceous, glabrous, somewhat glaucous beneath. Inflorescences terminal, solitary or paired, few-flowered; peduncles 1.5–7.5 cm. long; pedicels 1–2 cm. long. Flowers moderately large; calyx lobes lance-trigonal, 2.5–4.0 mm. long; corolla reflexed-rotate, dull red, the lobes 9–10 mm. long; gynostegium stipitate, yellow, orange, or reddish, the column cylindrical, about 2 mm. long and 1.5 mm. broad, the hoods broadly oblong, rounded at the tip, 5–6 mm. long, the basal horn narrowly acicular, somewhat shorter than the hood, arching over the anther head, the anther head narrowly conic, about 3 mm. long and 2.5 mm. broad, the wings conspicuously spurred at the base. Follicles erect on deflexed pedicels, narrowly fusiform, 8–10 cm. long, about 1 cm. thick, smooth, glabrous; seeds broadly oval, about 1 cm. long, the coma about 3.5 cm. long.

Brackish to fresh marshes, wet pine barrens, and low glades. Southern New Jersey to Florida and westward to eastern Texas. Flowering from May to August.

UNITED STATES:

ALABAMA: Mobile County.

DELAWARE: Kent and Sussex counties.

FLORIDA: Alachua, Baker, Bradford, Brevard, Broward, Calhoun, Charlotte, Citrus, Clay, Collier, Dade, Dixie, Duval, Flagler, Glades, Gulf, Hernando, Hillsborough, Lafayette, Lake, Lee, Levy, Manatee, Marion, Nassau, Osceola, Palm Beach, Pasco, Putnam, St. Johns, Taylor, Union, Volusia, and Washington counties.

GEORGIA: Brooks, Charlton, Glynn, Laurens, McIntosh, Sumter, and Wayne counties.

LOUISIANA: Calcasieu, Orleans, Rapides, and St. Tammany parishes.

MISSISSIPPI: Hancock, Harrison, Jackson, and Pearl River counties.

NORTH CAROLINA: Beaufort, Brunswick, Camden, Carteret, Chowan, Columbus, Currituck, Dare, Hyde, New Hanover, Pamlico, and Pasquotank counties.

NEW JERSEY: Cape May and Ocean counties.

SOUTH CAROLINA: Dorchester, Florence, Georgetown, Horry, Orangeburg, and Williamsburg counties.

TEXAS: Harris, Jefferson, and Orange counties.

VIRGINIA: Norfolk and Princess Anne counties.

It is rather remarkable that such closely related species as *A. rubra* and *A. lanceolata,* with so similar ranges and habitats and blooming at the same times of year, should maintain their genetic individualities so distinctly. Perhaps the differing anther wings provide the mechanical barriers to cross pollination.

Series 3. EXALTATAE

KEY TO THE SPECIES

a. Column narrowly cylindric, as long as broad or somewhat longer.
  b. Horn adnate to midway of the hood or below; leaves shortly petiolate to subsessile, ovate to ovate-lanceolate, subpalmately veined at the base. Tamaulipas to Sinaloa and southward to Veracruz and Guerrero .... 20. *A. ovata*
  bb. Horn adnate to near the tip of the hood; leaves rather long-petiolate, broadly elliptic, the venation typically pinnate throughout. Tamaulipas to Chiapas; Guatemala; Honduras; Nicaragua .... 21. *A. similis*
aa. Column shortly cylindrical to obconic, about half as long as broad.
  b. Median lobe of the hoods gradually rounded and entire; plants moderately stout and caulescent, more or less setose-hispidulous generally; leaves shortly petiolate and cordate typically. Tamaulipas to Sinaloa and southward to Chiapas; Guatemala; El Salvador .... 22. *A. contrayerba*

bb. Median lobe of the hoods truncate and more or less deeply dentate or lacerate.
  c. Peduncles typically much shorter than the subtending leaves, chiefly lateral; hoods delicately petalaceous; flowers white or the corolla slightly tinged with purple without.
    d. Plants relatively stout; leaves broadly elliptic to ovate. Southern Ontario; Maine to northern Georgia and westward to Minnesota and Iowa.............................23. *A. exaltat*
    dd. Plants relatively slender; leaves linear to filiform.
      e. Hoods about half longer than the anther head, broadly dentate; horn adnate to about midway of the hood; plants suffrutescent, essentially glabrous. Tamaulipas to San Luis Potosí ....24. *A. coulteri*
      ee. Hoods about as long as the anther head, deeply lacerate; horn adnate the entire length of the hood; plants herbaceous, minutely puberulent. Southern New Mexico and Arizona; Chihuahua and San Luis Potosí.....................25. *A. quinquedentata*
  cc. Peduncles typically much longer than the subtending leaves, chiefly terminal or subterminal; hoods rather fleshy; flowers greenish, usually deeply suffused with reddish purple.
    d. Plants relatively stout, essentially glabrous; leaves deeply cordate, sessile and amplexicaul; flowers relatively large, about 1.5 cm. long from hood- to corolla lobe-tip. New Hampshire to northern Florida and westward to Nebraska and eastern Texas ....26. *A. amplexicaulis*
    dd. Plants relatively small and subscapose, more or less densely pubescent; leaves obtuse to rounded at the base, distinctly petiolate.
      e. Inflorescence subterminal; flowers relatively large, about 1.5 cm. long from hood-to corolla lobe-tip. Nuevo Leon to Puebla..27. *A. virletii*
      ee. Inflorescences terminal; flowers relatively small, about 5 mm. long from hood-to corolla lobe-tip. Southern New Mexico (?); Coahuila, San Luis Potosí, and Zacatecas ....28. *A. scaposa*

20. ASCLEPIAS OVATA Mart. & Gal. in Bull. Acad. Roy. Brux. 11^1:363. 1844. [T.: *Galeotti 1554*, BR!]

Asclepias neglecta Hemsl. Biol. Centr.-Amer. Bot. 2:325. 1881. [T.: *Bourgeau 2714*, MO!]
Asclepias apocynifolia Woodson, in Amer. Jour. Bot. 22:687, *pl. 1, fig. 1.* 1935. [T.: *Bartlett 10264*, MO!]

Herbaceous perennials; stems moderately stout, simple, 3–9 dm. tall, generally but rather inconspicuously puberulent. Leaves opposite, rather shortly petiolate, ovate to ovate-lanceolate, acuminate to broadly acute at the tip, broadly rounded to slightly cordate at the base, 6–16 cm. long, 2–9 cm. broad, membranaceous, inconspicuously puberulent to glabrate above and beneath; petioles 0.7–1.0 cm. long.

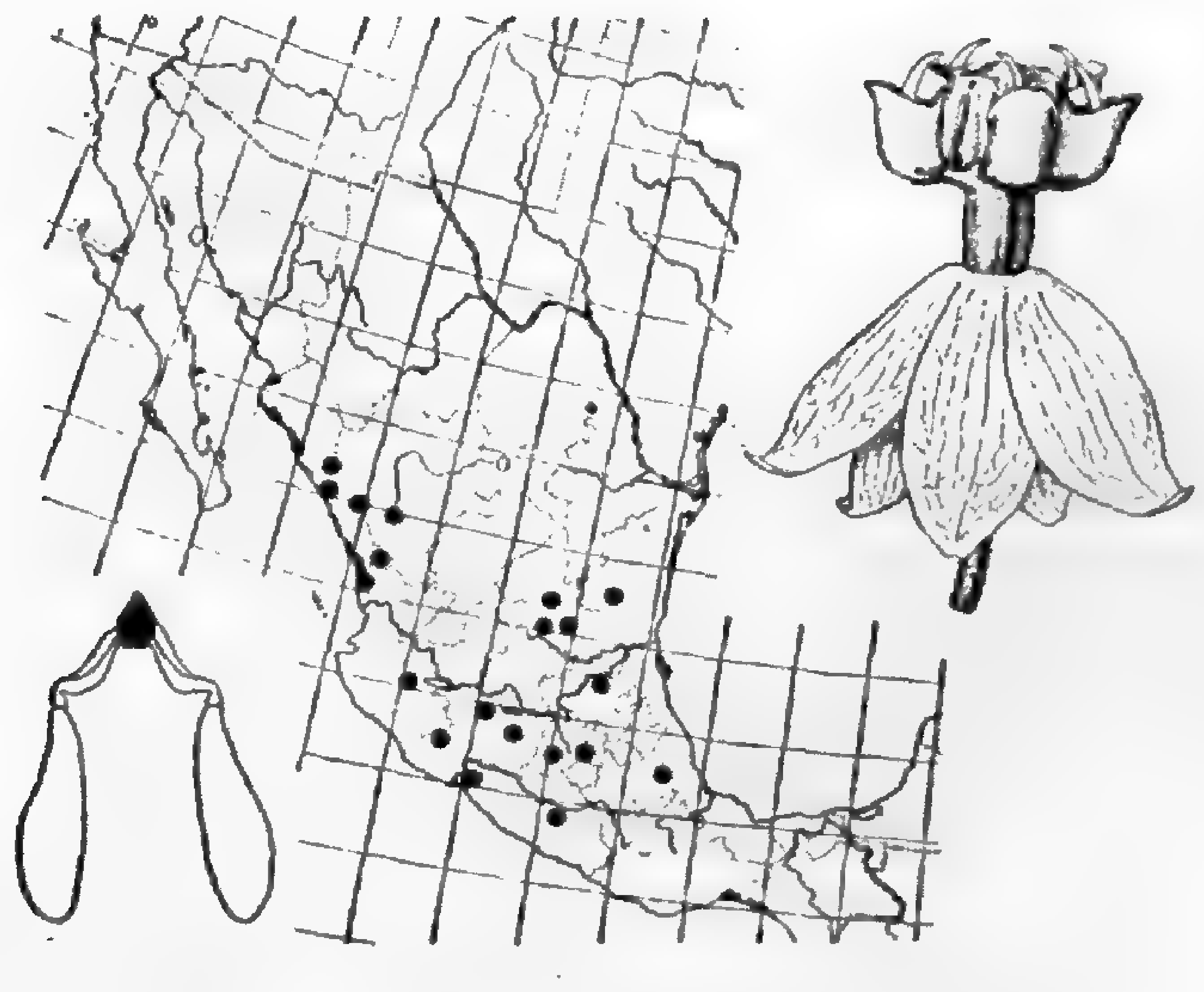

Fig. 26. *Asclepias ovata* Mart. & Gal.

Inflorescences solitary at the upper few or several nodes, several- to many-flowered; peduncles 2–7 cm. long; pedicels 1.5–2.0 cm. long. Flowers rather small; calyx lobes narrowly trigonal, 3–5 mm. long, sparsely pilosulose to glabrate; corolla reflexed-rotate, greenish white sometimes suffused with purple or rose, the lobes 6–9 mm. long; gynostegium white, narrowly stipitate, the column 1–2 mm. long, 1.5–2.0 mm. broad, the hoods rhombic with the median lobe broadly rounded and entire, 2–5 mm. long, the horn adnate to about midway of the hood, narrowly acicular, about half longer than the hood, arching gradually over the anther head, the anther head cylindrical, 2.5–3.0 mm. long and broad. Follicles erect on deflexed pedicels, rather narrowly fusiform, 7–9 cm. long, 1.0–1.6 cm. broad, smooth, glabrous; seeds oval, 5–6 mm. long, the pale tawny coma 2–3 cm. long.

Open pine and oak forests particularly on hillsides and in canyons. Central Mexico from Tamaulipas to Sinaloa and southward to Veracruz and Guerrero. Flowering from June to September.

MEXICO: DISTRITO FEDERAL: Santa Fé, Valley of Mexico, Pedregal de San Angel. DURANGO: Cacaria. GUERRERO: Chilpancingo, Montes de Oca. GUANAJUATO: Guanajuato. HIDALGO: Jacala. JALISCO: Hacienda San Marcos, Autlán. MEXICO: Temascaltepec, Lechería. MICHOACAN: Zacapu, Apatzingan. NAYARIT: Tepic, Acaponeta, Pedro Paulo. SAN LUIS POTOSÍ: Alvarez, Las Canoas, Bagre. SINALOA: San Ignacio, Las Mesas, Quebrado de Mansana. TAMAULIPAS: Jaumave. VERACRUZ: Orizaba.

Although variable, *A. ovata* is a very distinctive species particularly by reason of the leaf venation which appears as somewhat palmate because of the aggregation of the basal 3–4 secondary veins toward the base of the midrib. This is fortunate, since the holotype (in Herb. Brux.) consists only of a fragment of the upper portion of a stem bearing three somewhat damaged leaves; these, however, show the characteristic venation.

21. **Asclepias similis** Hemsl. Biol. Centr.-Amer. Bot. 2:326. 1881. [T.: *Ghiesbreght 665*, MO!]

Asclepias bidentata Hemsl. loc. cit. 322. 1881. [T.: *Coulter 985*, K!]
Asclepias alticola Fourn. in Ann. Sci. Nat. Ser. VI, 14:371. 1882. [T.: *Ghiesbreght 34*, K!]
Asclepias guatemalensis Donn. Sm. in Bot. Gaz. 18:207. 1893. [T.: *R. Gomez s. n.*, US!]

Herbaceous perennials from a rather tuberous rootstalk. Stems rather stout, simple, 2–13 dm. tall, rather inconspicuously puberulent. Leaves opposite, usually rather long-petiolate, broadly elliptic, apex rather shortly but narrowly acuminate, base obtuse to broadly acute, firmly membranaceous, dark green above, glaucous and inconspicuously pilosulose beneath; petioles 0.5–2.5 cm. long. Inflorescences solitary at the uppermost nodes, frequently terminal and paired, several- to many-flowered; peduncles 2–6 cm. long, rather stout; pedicels slender, 1.5–2.5 cm. long. Flowers moderately large; calyx lobes lance-trigonal, 4–6 mm. long, sparsely pilosulose to glabrous; corolla reflexed-rotate, greenish white or cream, the lobes 7–10 mm. long; gynostegium rather narrowly stipitate, greenish white to cream, the corona occasionally tinged with purple at the base, the column cylindrical, 1.5–2.0 mm. long, about 2 mm. broad, the hoods very broadly oval, with the median lobe very broadly rounded and entire, the horn adnate to near the tip of the hood, acicular, arching over the anther head, the anther head brown, rather broadly cylindric, 3–4 mm. long, 3.0–3.5 mm. broad. Follicles erect on deflexed pedicels, rather narrowly fusiform, 8–15 cm. long, about 2 cm. thick, smooth, finely and densely puberulent; seeds broadly oval, 5–8 mm. long, the white coma 3.5–5.0 cm. long.

Open oak and pine woods and thickets, hillsides and along arroyos. Eastern Mexico from Tamaulipas to Chiapas; Guatemala; Honduras; Nicaragua. Flowering from June to December.

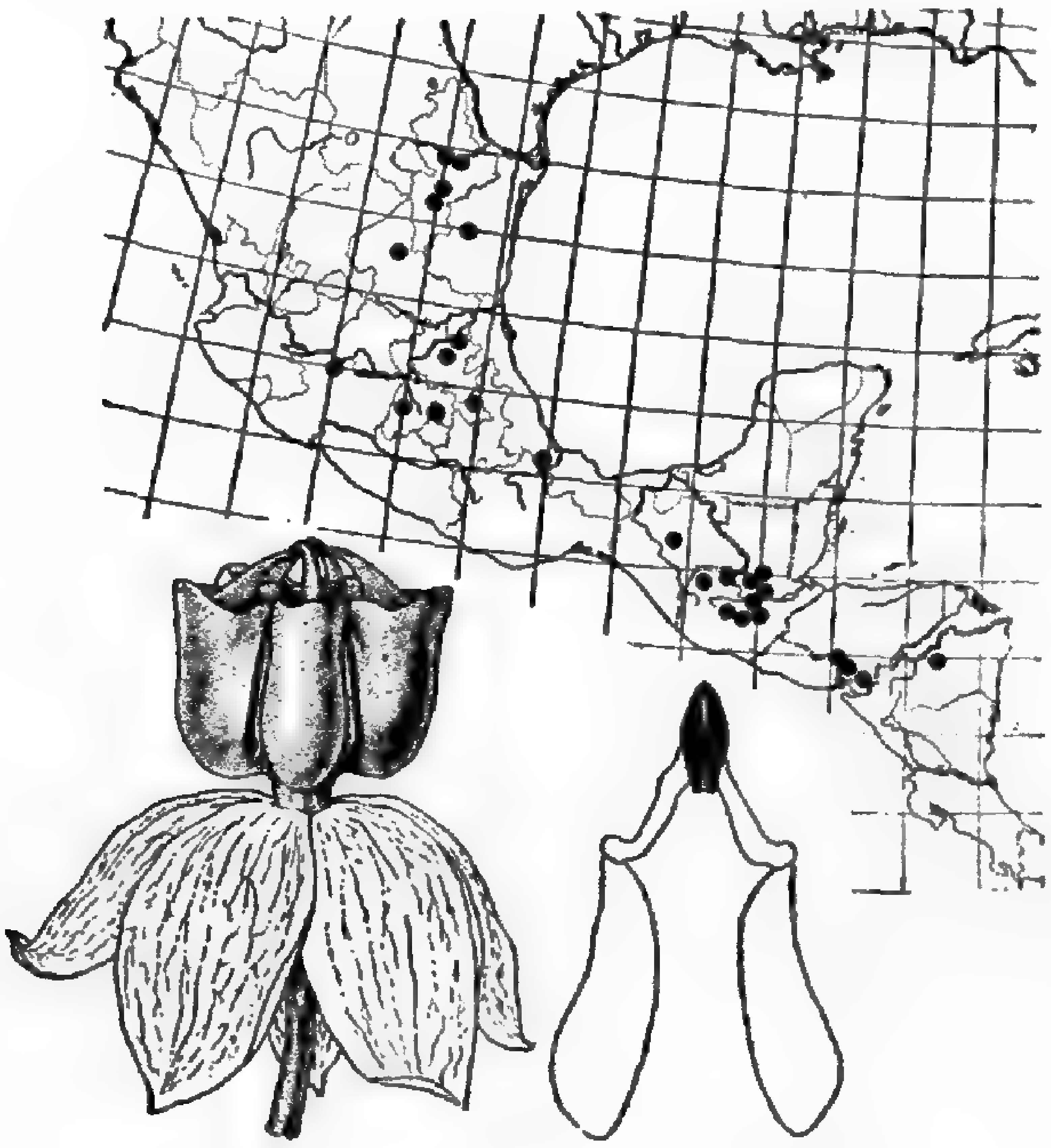

Fig. 27. *Asclepias similis* Hemsl.

MEXICO: CHIAPAS: Siltepec, El Pozo. GUERRERO: Taxco. HIDALGO: Jacala, Zacualtipán. MEXICO: Valley of Mexico. MICHOACAN: Zacapu. NUEVO LEÓN: Dulces Nombres, Villa Santiago, Monterrey, Galeana. SAN LUIS POTOSÍ: Alvarez. TAMAULIPAS: San José. TLAXCALA: San Antonio. VERACRUZ: Sta. Lucrecía.

GUATEMALA: ALTA VERAPAZ: Coban, Samac. CHIMALTENANGO: Tecpam, Alameda, Patzúm, Chimaltenango. GUATEMALA: San Juan Sacatepéquez. HUEHUETENANGO: Cerro Pixpix, Chiantla, Las Palmas, San Sebastián H., Huehuetenango. JALAPA: Jalapa, Paraíso, La Laguna. QUICHÉ: Nebaj. SACATEPÉQUEZ: Pastores. SOLOLÁ: San Pedro. ZACAPA: Sierra de las Minas, Sierra de Monos.

HONDURAS: CHOLUTECA: San Marcos. COMAYAGUA: Siguatepeque. MORAZAN: El Zamorano, Mt. Uyuca, Agua Amarilla.

NICARAGUA: JINOTEGA: La Montañita, Las Mesitas, Cerro de la Cruz.

In northern Mexico, in the range of *A. ovata*, specimens of *A. similis* tend to resemble that species somewhat in having leaves that are less glaucous beneath (although no definite tendency to the subpalmate veins), flowers that are somewhat smaller, and in other less tangible respects. It seems possible that occasional hybridization might produce this effect without actually prompting the species to merge as in a genocline.

22. Asclepias contrayerba Sessé & Moc. Fl. Mex. ed. 1, 2:79. 1887. [T.: *Sessé & Mociño 1274*, F!]

Asclepias setosa Benth. Pl. Hartw. 24. 1839, non Forsk. [T.: *Hartweg 213*, K!]
Asclepias jaliscana Robinson, in Proc. Amer. Acad. 29:318. 1894. [T.: *E. Palmer 20*, MO!]

Herbaceous perennials from a thick tuberous rootstalk. Stems clustered from the rootstalk, relatively slender, simple or occasionally branching from near the base, frequently decumbent, 1.5–6.0 dm. tall, usually conspicuously setose-hispidulous, rarely glabrate. Leaves opposite, very shortly petiolate, broadly ovate to narrowly oblong-lanceolate, apex acute to obtuse, base broadly cordate to rounded, 3–12 cm. long, 1.0–4.5 cm. broad, firmly membranaceous, glaucous, frequently more or less crispate, setose-hispidulous or infrequently glabrate; petioles 2–4 mm. long. Inflorescences terminal and solitary or clustered corymbosely at the uppermost nodes, several- to many-flowered; peduncles 2–7 cm. long; pedicels 1–3 cm. long. Flowers rather small; calyx lobes ovate-lanceolate, 5–6 mm. long, minutely pilosulose; corolla pale greenish or greenish white, frequently tinged with purplish brown, the lobes 7–10 mm. long; gynostegium rather shortly stipitate, white or cream, the column rather broadly cylindrical, about 2 mm. long and broad, the hoods broadly rhombic with the median lobe gradually rounded and entire, 3–6 mm. long, the horn adnate below midway, slightly longer than the hood, arching over the anther head, the anther head broadly cylindric, 2.5–3.0 mm. long and broad. Follicles erect on deflexed pedicels, fusiform, 6–11 cm. long, 1.5–2.5 cm. broad, smooth, more or less densely setose-hispidulous; seeds oval, about 5 mm. long, the pale tawny coma about 3.5 cm. long.

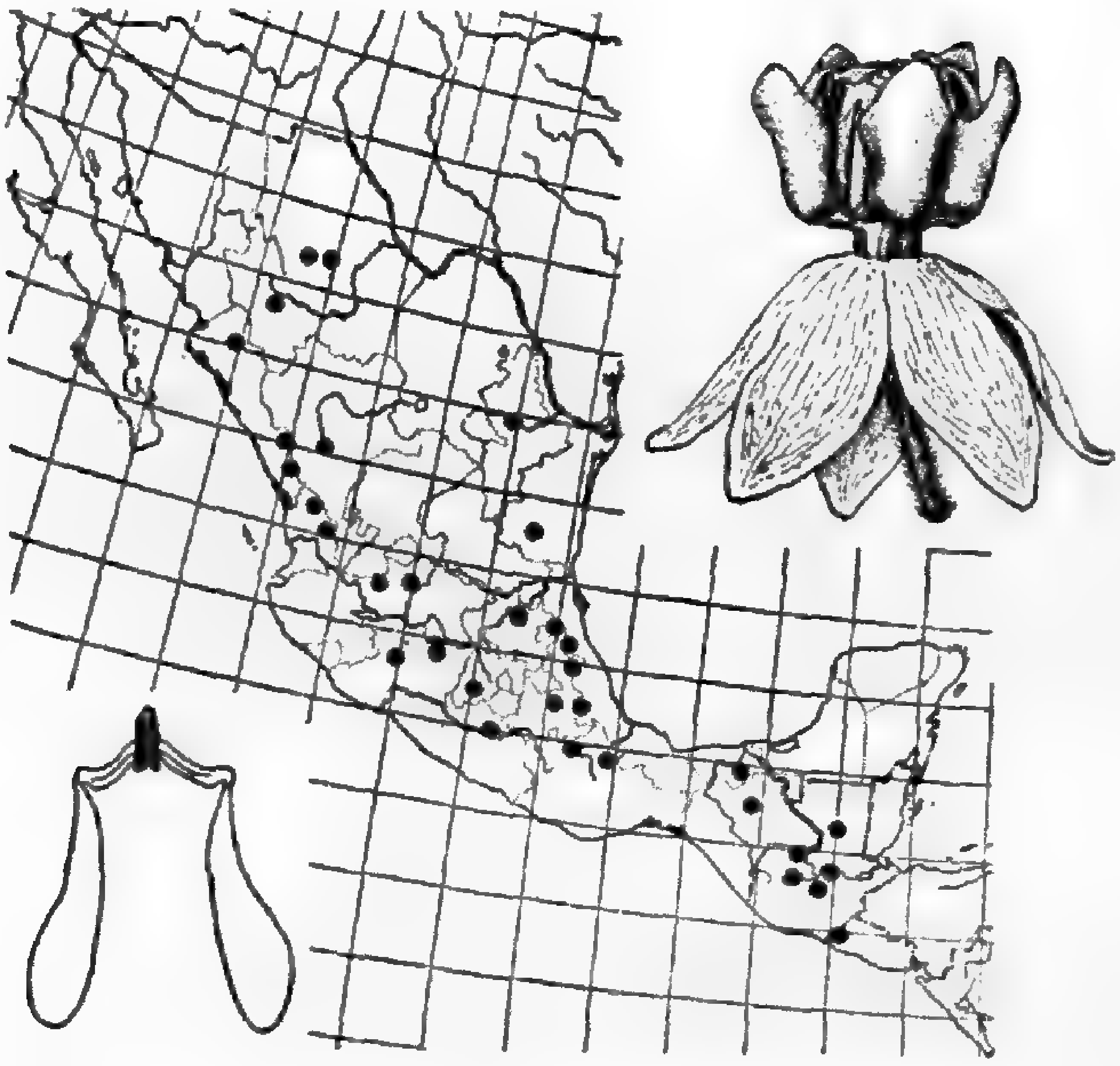

Fig. 28. *Asclepias contrayerba* Sessé & Moc.

Plains, hillsides, and barrancas, in open oak woods, thickets, and grass. Central Mexico from Tamaulipas to Sinaloa and southward to Chiapas; Guatemala; El Salvador. Flowering from May to September.

MEXICO: CHIHUAHUA: Mojarachic, Colonia García, Chihuahua. CHIAPAS: Las Casas. DURANGO: Otinapa, Cacaria. GUERRERO: Mina. HIDALGO: Jacala. JALISCO: Guadalajara, Río Blanco, León. MEXICO: Lechería, Temascaltepec. MICHOACAN: Morelia, Tancitaro. NAYARIT: Aguacate, Dolores, Acaponeta, Pedro Paulo. NUEVO LEÓN: Dulces Nombres. OAXACA: Nochixtlan, Cuicatlan, Santo Domingo. PUEBLA: San Baltazar, Esperanza. SINALOA: Cerro Colin, San Pedro, Colomos, Rosario. TABASCO: Estapilla. TAMAULIPAS: Jaumave. VERACRUZ: La Palmilla, Zacuapan, Orizaba.

GUATEMALA: GUATEMALA: Chillani, Guatemala. HUEHUETENAGO: Aguacatán. JALAPA: Montaña Durazno. PETÉN: La Libertad. SOLOLÁ: Volcán San Pedro.

EL SALVADOR: AHUACHAPAN: Cerro de San Jacinto.

It is unfortunate that Bentham's name is antedated by Forskal's; the application of Sessé's & Mociño's is directed by two specimens collected by the authors now in the herbarium of the Chicago Natural History Museum. *Contrayerba* apparently is quite an appropriate name for this very distinctive species, for the plants are still known by that name in the State of Mexico, according to Hinton, who has also found the name *lechetresno* applied to it. In Guatemala the plant is known as *sicaquina, jicaca,* and *jicaquina,* and it is reputed to be a sternutatory for colds. In El Salvador a name reported is *ishcaco.*

23. ASCLEPIAS EXALTATA L. Amoen. Acad. 3:404. 1756, ex char.

Asclepias syriaca β exaltata L. Sp. Pl. ed. 2, 313. 1762.
Asclepias polystachia Walt. Fl. Carol. 107. 1788, ex char. [T.: Fraser Herb., Brit. Mus.!]
Asclepias phytolaccoides Pursh, Fl. Amer. Sept. 1:180. 1816, ex char.
Asclepias bicknellii Vail, in Bull. Torrey Bot. Club 31:458, *pl. 19.* 1904. [T.: *Bicknell s. n.*, NY!]

Herbaceous perennials. Stems relatively stout, simple, 4–10 dm. tall, glabrous or inconspicuously pilosulose in decurrent lines from the nodes. Leaves opposite, petiolate, ovate to elliptic or oblong-elliptic, apex shortly but narrowly acuminate, base broadly obtuse, 10–20 cm. long, 2–11 cm. broad, thinly membranaceous, scatteringly pilosulose to glabrate above, glaucous beneath; petioles 0.5–1.5 cm. long. Inflorescences subterminal and solitary at the upper nodes, several- to many-flowered; peduncle relatively stout, 0.3–8.5 cm. long; pedicels slender, 3.5–5.0 cm. long. Flowers moderately large; calyx lobes ovate-lanceolate, about 5 mm. long, essentially glabrous; corolla reflexed-rotate, white usually flushed with rose or purple without, the lobes 8–12 mm. long; gynostegium rather shortly stipitate, white, the column narrowly obconic to cylindric, about 2 mm. long and broad, the hoods tubular-cucullate, more or less conspicuously denticulate, 3.5–4.0 mm. long, the horn adnate below the middle, nearly twice as long as the hood and arching over the anther head, the anther head cylindric, 3.0–3.5 mm. long and broad. Follicles erect on deflexed pedicels, rather narrowly fusiform, 12–15 cm. long, 1.5–2.0 cm. broad, smooth, essentially glabrous; seeds broadly oval, 7–9 mm. long, the white coma 3.0–4.5 cm. long.

Moist woods, meadows, and copses. Southern Ontario; Maine to Georgia and westward to Minnesota and Iowa. Flowering from May to August.

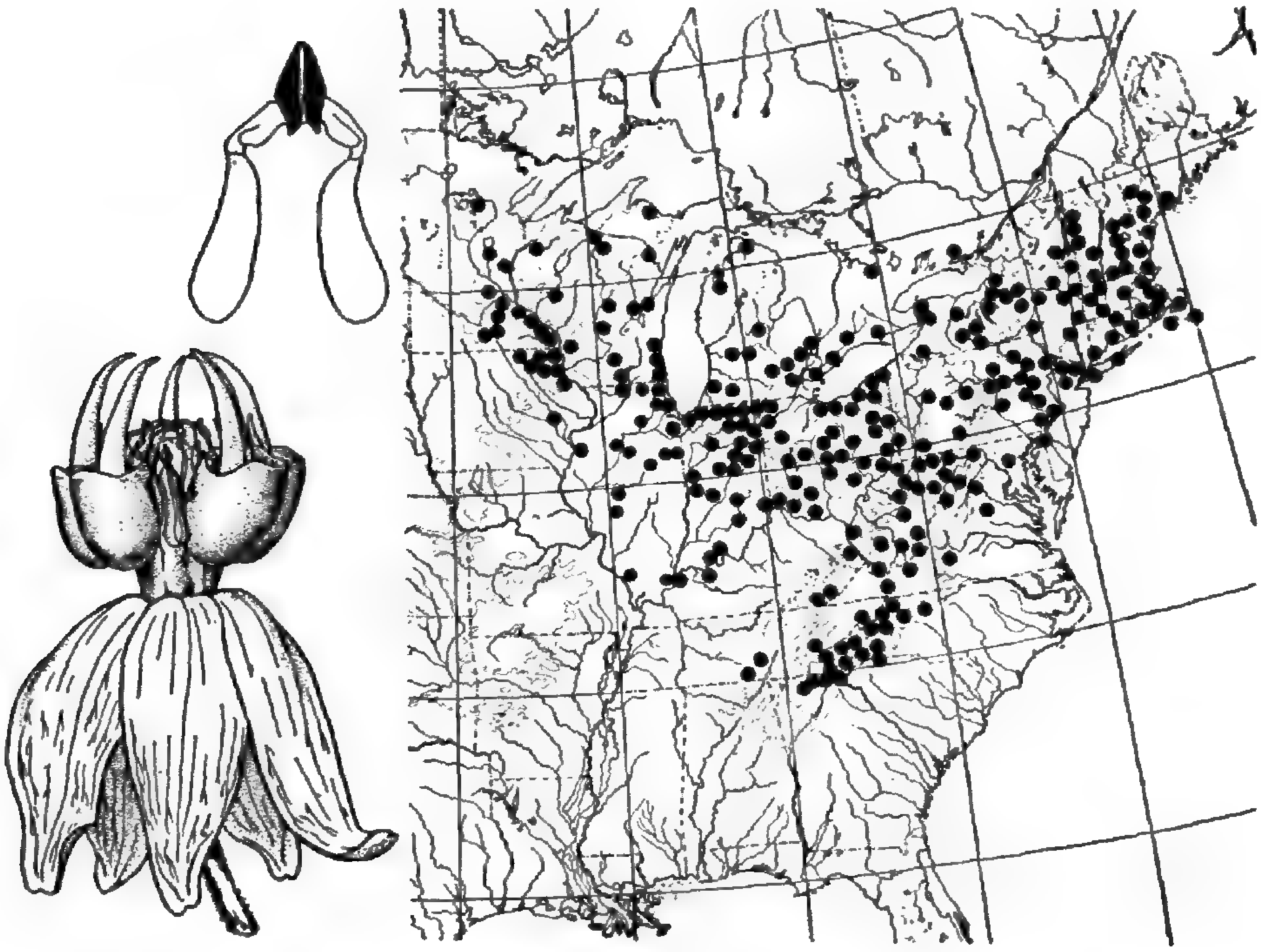

Fig. 29. *Asclepias exaltata* L.

CANADA: ONTARIO: Elgin, Hastings, Lambton, East, Middlesex, Norfolk, and Simcoe counties.

UNITED STATES:

CONNECTICUT: Fairfield, New Haven, New London, and Tolland counties.

DELAWARE: New Castle County.

GEORGIA: Fannin, Gilmer, Rabun, and Towns counties.

ILLINOIS: Champaign, Cook, Du Page, Hardin, Henderson, Jackson, Johnson, Kankakee, Lake, La Salle, Macon, McHenry, Macoupin, Menard, Peoria, Tazewell, Union, Vermilion, Will, and Winnebago counties.

INDIANA: Allen, Bartholomew, Blackford, Cass, Crawford, Dearborn, Elkhart, Fountain, Grant, Hamilton, Hendricks, Huntington, Jackson, Kosciusko, Lagrange, Lake, La Porte, Madison, Noble, Parke, Perry, Porter, St. Joseph, Steuben, Wells, and Whitley counties.

IOWA: Allamakee, Chickasaw, Clayton, Dubuque, Fayette, Johnson, Mitchell, and Winneshiek counties.

KENTUCKY: Bell, Hancock, Harlan, Martin, and Union counties.

MAINE: Androscoggin, Cumberland, Lincoln, Oxford, and York counties.

MARYLAND: Garrett and Howard counties.

MASSACHUSETTS: Barnstable, Berkshire, Bristol, Dukes, Essex, Franklin, Hampden, Hampshire, Middlesex, Nantucket, Norfolk, Plymouth, Suffolk, and Worcester counties.

MICHIGAN: Cheboygan, Grand, Gratiot, Ingham, Ionia, Kalamazoo, Kent, Livingston, Macomb, Marquette, St. Clair, Van Buren, and Washtenaw counties.

MINNESOTA: Cass, Chisago, Goodhue, Hennepin, Houston, Mille Lacs, Ramsey, Rice, Scott, Steele, Wabasha, Waseca, and Winona counties.

NEW HAMPSHIRE: Belknap, Carroll, Cheshire, Grafton, Hillsborough, Merrimack, Rockingham, and Strafford counties.

NEW JERSEY: Bergen, Morris, Somerset, and Sussex counties.

NEW YORK: Albany, Cattaraugus, Cayuga, Chenango, Columbia, Delaware, Erie, Madison, Montgomery, Niagara, Oneida, Onondaga, Ontario, Oswego, Otsego, Queens, Rensselaer, Schuyler, Suffolk, Tioga, Tompkins, Ulster, Warren, and Washington counties.

NORTH CAROLINA: Ashe, Buncombe, Burke, Forsyth, Graham, Haywood, Henderson, Jackson, Macon, Mitchell, Polk, Rutherford, Swain, and Watauga counties.

OHIO: Adams, Ashtabula, Athens, Auglaize, Belmont, Carroll, Clark, Clermont, Coshocton, Columbiana, Cuyahoga, Defiance, Delaware, Erie, Franklin, Geauga, Greene, Hamilton, Highland, Hocking, Knox, Lake, Licking, Lorain, Madison, Medina, Monroe, Perry, Richland, Stark, and Williams counties.

PENNSYLVANIA: Bedford, Berks, Blair, Cambria, Carbon, Centre, Delaware, Fayette, Indiana, Luzerne, Lycoming, Monroe, Northampton, Perry, Philadelphia, Pike, Schuylkill, Snyder, and Sullivan counties.

RHODE ISLAND: Providence County.

TENNESSEE: Blount, Franklin, Grundy, and Unicoi counties.

VERMONT: Addison, Chittenden, Rutland, Windham, and Windsor counties.

VIRGINIA: Bedford, Giles, Orange, Page, and Smyth counties.

WEST VIRGINIA: Calhoun, Grant, Greenbrier, Hardy, Harrison, McDowell, Monongalia, Monroe, Morgan, Ohio, Pendleton, Preston, Raleigh, Randolph, Summers, Upshur, Wayne, and Wetzel counties.

WISCONSIN: Adams, Brown, Dane, Eau Claire, Marinette, Milwaukee, Oneida, Outagamie, Ozaukee, Portage, Racine, Rock, Vernon, Vilas, and Washburne counties.

This species, commonly known as poke milkweed, usually has been named *A. phytolaccoides* (hence the common name) or *A. exaltata* "(L.) Muhl." The bibliography here follows the discussion of Fernald and Schubert in Rhodora 50:218–220. 1948.

24. ASCLEPIAS COULTERI A. Gray, in Proc. Amer. Acad. 12:71. 1877. [T.: *Coulter 983*, GH!]

Asclepias tithymaloides Greene, in Erythea 1:151. 1893. [T.: *Pringle 3786*, MO!]

Suffrutescent perennials. Stems relatively slender, simple or branching, 3–6 dm. tall, glabrous or very inconspicuous pilosulose when very young. Leaves opposite, sessile, linear to filiform, 5–13 cm. long, 1–6 mm. broad, firmly membranaceous, glabrous. Inflorescences solitary at the uppermost nodes, few-flowered; peduncles 1–3 cm. long, slender; pedicels 2.0–2.5 cm. long. Flowers moderately large; calyx lobes lance-trigonal, 2–3 mm. long; corolla reflexed-rotate, greenish white, frequently somewhat suffused with rose without at the tips, the lobes 7–9 mm. long; gynostegium rather shortly stipitate, white or cream, the column narrowly obconic, 1.25–1.5 mm. long, 1.75–2.0 mm. broad, the hoods tubular-cucullate, broadly dentate, 3.5–4.025 mm. long, the horn about half adnate to the hood and slightly longer than it, only slightly arching, the anther head narrowly conic, about 2 mm. long and 2.5 mm. broad. Follicles erect on deflexed pedicels, narrowly fusiform, 4–5 cm. long, about 7 mm. broad, smooth, glabrous and somewhat glaucous; seeds oval, about 3 mm. long, the white coma about 2 cm. long.

Dry limestone ledges. Northeastern Mexico. Flowering from May to August.

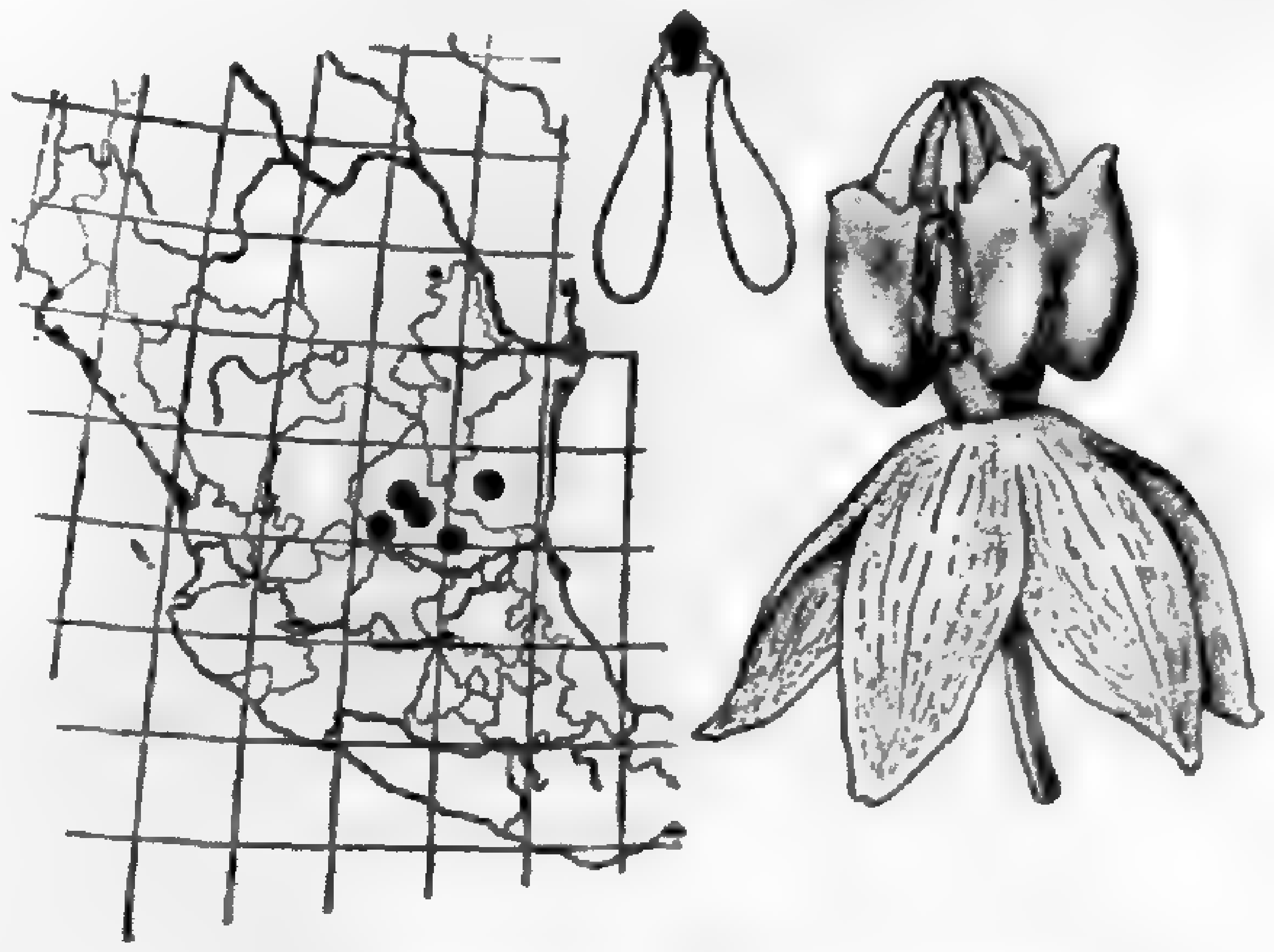

Fig. 30. *Asclepias coulteri* A. Gray

MEXICO: SAN LUIS POTOSÍ: Minas de San Rafael, Las Palmas, Sierra de Guascama, Rascón. TAMAULIPAS: Jaumave.

25. ASCLEPIAS QUINQUEDENTATA A. Gray, in Proc. Amer. Acad. 12:71. 1877. [T.: *Wright 1689*, MO!]

Asclepias quinquedentata var. *neomexicana* Greene, ex A. Gray, loc. cit. 16:103. 1881. [T.: *Greene s. n.*, MO!]
Asclepias schaffneri A. Gray, loc. cit. 1881. [T.: *Schaffner 56*, GH!]
Asclepias palmeri Vail, in Bull. Torrey Bot. Club 25:171. 1899. [T.: *Parry & Palmer 583*, MO!]
Asclepias amsonioides Standl. in Field Mus. Publ. Bot. 22:44. 1940. [T.: *LeSueur 848*, MO!]

Herbaceous perennials from rather deep, tuberous rootstalks. Stems relatively slender, simple above, branching rather caespitosely below, the basal branches usually dwarf and sterile, 1.5–3.0 dm. tall, minutely and generally puberulent, rarely glabrate. Leaves opposite, sessile or subsessile, linear to filiform, 4–9 cm. long, 1–2 mm. broad, minutely and scatteringly pilosulose or puberulent. Inflorescences subterminal from few of the uppermost nodes, few-flowered; peduncles rather slender, 1–8 cm. long; pedicels slender, 1.5–2.0 cm. long. Flowers rather small; calyx lobes lance-trigonal, about 2 mm. long, minutely pilosulose to glabrate; corolla reflexed-rotate, pale green usually flushed with rose or purple without, the lobes 5–6 mm. long; gynostegium shortly stipitate, greenish white, the column narrowly obconic, about 1 mm. long and 1.5 mm. broad, the hoods cylindrical-cucullate, sharply erose, about 3 mm. long, the horns completely adnate to the hoods and about half longer than they, ascending and scarcely arching, the anther head cylindric, about 2 mm. long and broad. Follicles erect on deflexed pedicels, narrowly fusiform, 7–10 cm. long, 0.5–0.8 cm. thick, smooth, minutely puberulent; seeds oval, 5–7 mm. long, the pale tawny coma 3–4 cm. long.

Rocky hills and arroyos. Southern Arizona and New Mexico; Chihuahua to San Luis Potosí. Flowering from June to August.

UNITED STATES:

ARIZONA: Cochise, Coconino, and Pima counties.

NEW MEXICO: Grant and Socorro counties.

MEXICO: CHIHUAHUA: Sierra Madre, El Cima, Colonia Garcia, Chihuahua, Madera. SAN LUIS POTOSÍ: Morales, San Luis Potosí.

In San Luis Potosí the specimens are rather atypical, and I suspect that hybridization with *A. coulteri* may be to blame. Even if such is not the case, however, and the variation is geographic, I am quite unwilling to recognize more than one species in the complex.

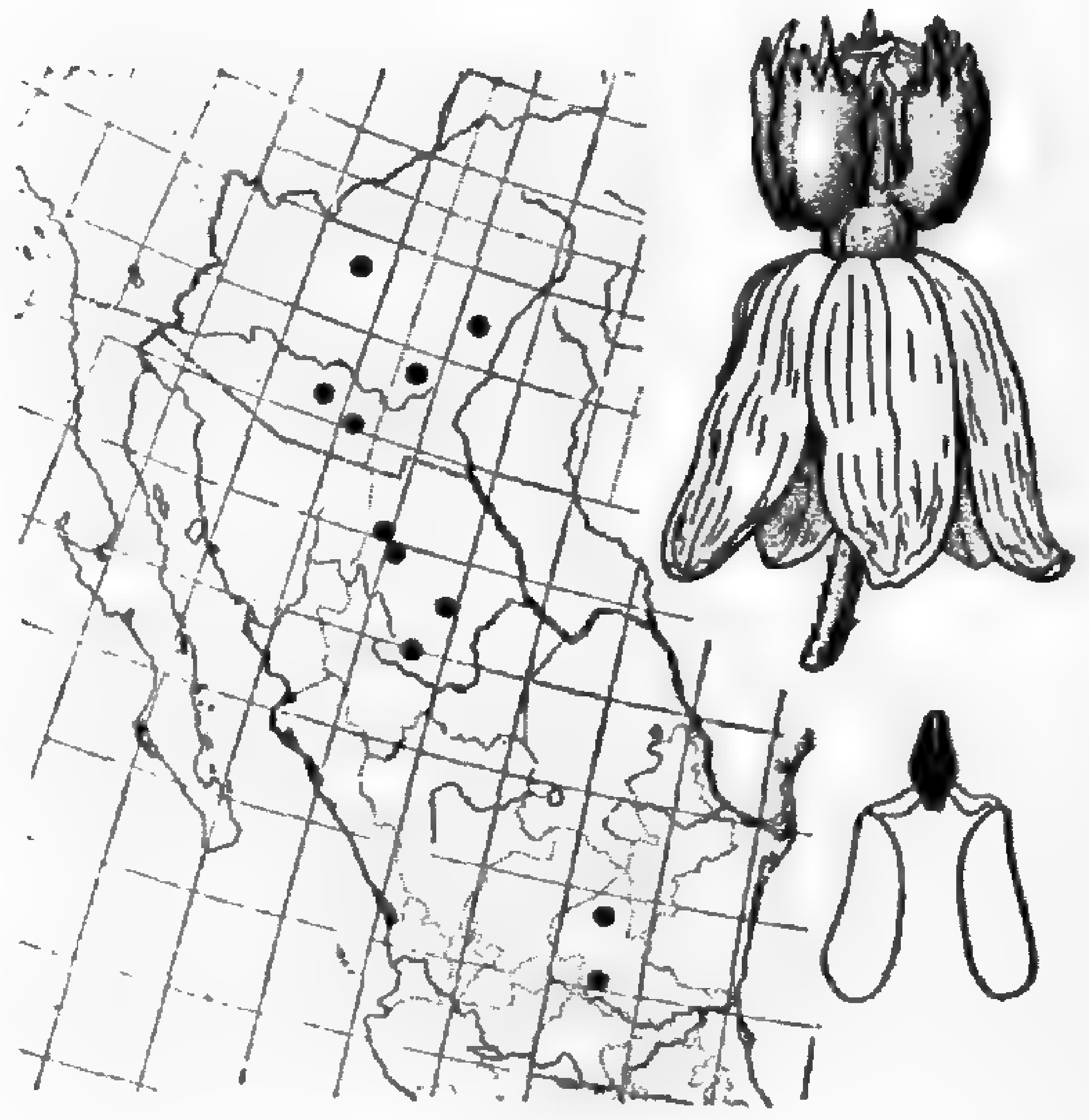

Fig. 31. *Asclepias quinquedentata* A. Gray

26. Asclepias amplexicaulis Sm. in Abbott & Sm. Nat. Hist. Lepidopt. Insects Ga. 1:*pl. 7.* 1797, ex ic.

Asclepias obtusifolia Michx. Fl. Bor.-Amer. 1:115. 1803, ex char.
Asclepias rotundifolia Raf. Atl. Jour. 1:152. 1832, ex char.
Asclepias gladewitzii Farwell, in Amer. Midl. Nat. 12:128. 1930. [T.: *Farwell 8229,* NY!]

Herbaceous perennials. Stems stout, simple, 4–9 dm. tall, glabrous. Leaves opposite, sessile, broadly ovate or oval to oblong-lanceolate, apex broadly rounded to obtuse, frequently mucronate, base broadly cordate and amplexicaul, rather thickly membranaceous or subcoriaceous, more or less glaucaus, frequently crispate. Inflorescences terminal and solitary, rather rarely lateral also from the uppermost node, usually many-flowered; peduncles stout, 10–30 cm. long, shorter when lateral; pedicels rather stout, 2–5 cm. long. Flowers rather large; calyx lobes lanceolate, 3–5 mm. long, glabrous; corolla reflexed-rotate, greenish more or less deeply suffused with purple or rose, the lobes 9–11 mm. long; gynostegium pale purple or rose, rather shortly stipitate, the column cylindrical, about 2 mm. long, 2.5–3.0 mm. broad, the hoods tubular-cucullate, rather indistinctly dentate to essentially entire, about 5 mm. long, the horn adnate below the middle, rather stoutly acicular, about half longer than the hood, broadly arching over the anther head, the anther head broadly cylindrical, 3.0–3.5 mm. long, about 3 mm. broad. Follicles erect on deflexed pedicels, rather narrowly fusiform, 10–16 cm. long, about 1–2 cm. thick, smooth, glabrous and rather glaucous; seeds broadly oval, 6–9 mm. long, the pale tawny coma 4–6 cm. long.

Open woods, prairies, old sand dunes, spreading to clearings, meadows, pastures, roadsides, and railways, chiefly in sandy or gravelly soil. New Hampshire to Florida, westward to Nebraska and Texas. Flowering from March to September.

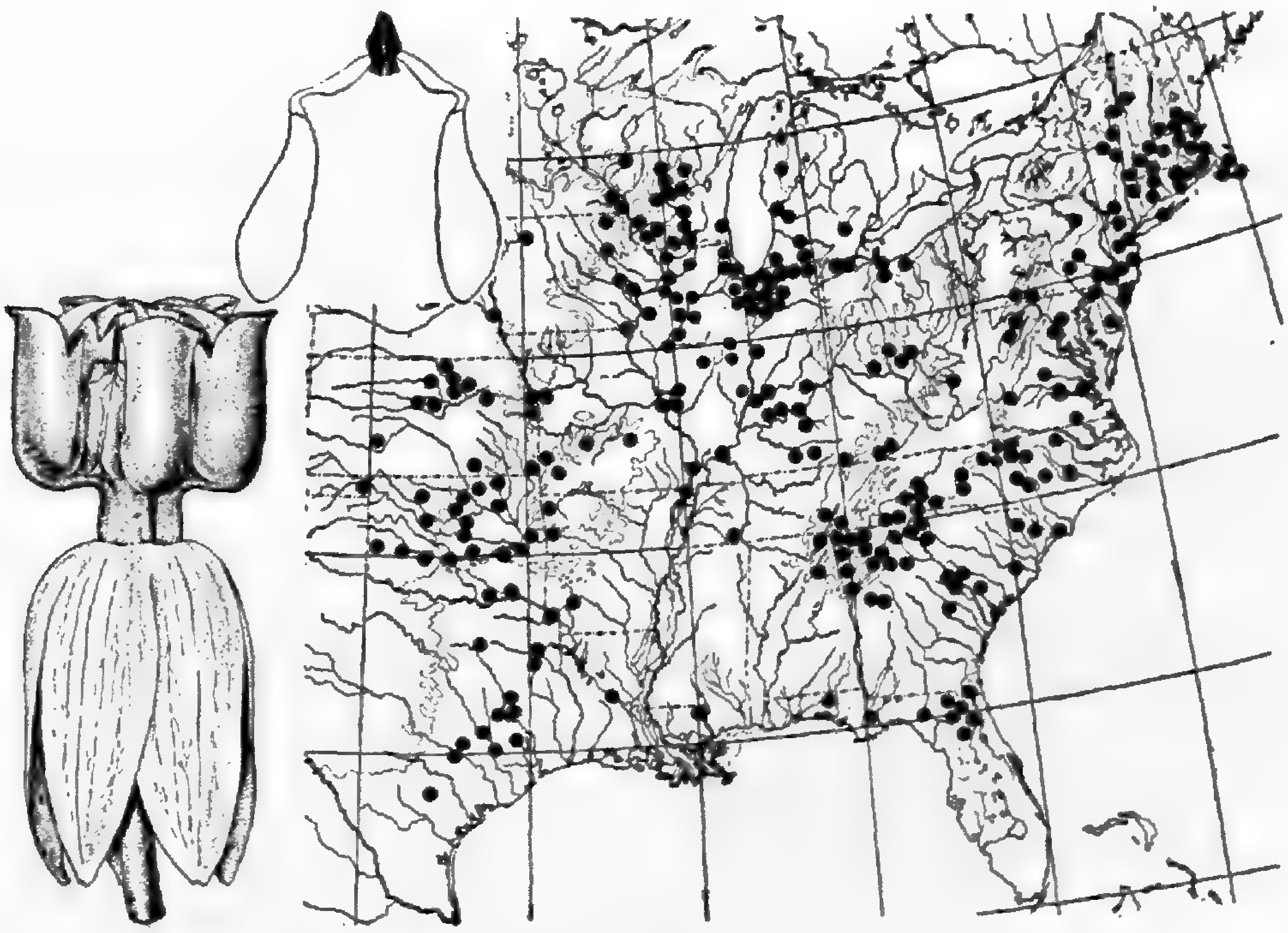

Fig. 32. *Asclepias amplexicaulis* Sm.

United States:

alabama: Etowah and Jackson counties.

arkansas: Nevada, Sebastian, and Washington counties.

connecticut: Hartford, New Haven, New London, and Windham counties.

delaware: New Castle and Sussex counties.

florida: Alachua, Bradford, Columbia, Duval, Lafayette, Liberty, Marion, Putnam, and Walton counties.

georgia: Campbell, Clarke, Columbia, Dade, De Kalb, Emanuel, Floyd, Forsyth, Gilmer, Gwinnett, Haralson, Meriwether, Murray, Richmond, Upson, Walker, and White counties.

iowa: Black Hawk, Johnson, Lee, Muscatine, Palo Alto, and Winneshiek counties.

illinois: Champaign, Coles, Cook, Du Page, Henderson, Iroquois, Jo Daviess, Kankakee, Lake, Lee, Madison, Mason, Marshall, Massac, Peoria, St. Clair, Sangamon, Stark, Tazewell, Wabash, and Whiteside counties.

indiana: Benton, Daviess, Elkhart, Fulton, Harrison, Jasper, Knox, Lagrange, Lake, Marshall, Newton, Perry, Porter, Pulaski, St. Joseph, Spencer, Starke, Steuben, Vigo, Washington, and White counties.

kansas: Chautauqua, Cherokee, Clay, Cloud, Edwards, Ellsworth, Miami, Pottawatomie, Riley, Saline, Wabaunsee, Washington and Wyandotte counties.

louisiana: Rapides and Washington parishes.

kentucky: Barren, Bell, Hardin, Harlan, Lyon, McCreary, and Warren counties.

maryland: Prince Georges County.

massachusetts: Barnstable, Berkshire, Bristol, Dukes, Essex, Franklin, Hampden, Hampshire, Middlesex, Nantucket, Norfolk, Plymouth, and Worcester counties.

minnesota: Houston and Winona counties.

michigan: Cass, Kalamazoo, Kent, Lake, Livingston, Muskegon, and St. Joseph counties.

missouri: Dent, Dunklin, Jackson, Jasper, Lawrence, St. Louis, and Scott counties.

nebraska: Douglas County.

new hampshire: Cheshire, Hillsborough, Merrimack, and Rockingham counties.

new jersey: Atlantic, Burlington, Camden, Cape May, Gloucester, Middlesex, Monmouth, Ocean, and Passaic counties.

new york: Albany, Columbia, Dutchess, Orange, Richmond, Saratoga, Schenectady, Suffolk, and Warren counties.

north carolina: Alexander, Brunswick, Buncombe, Catawba, Durham, Forsyth, Green, Guilford, Halifax, Haywood, Hoke, Jackson, Johnston, Macon, Madison, Moore, Orange, and Rockingham counties.

ohio: Adams, Erie, Fulton, Gallia, Huron, Jackson, Lorain, Lucas, and Ross counties.

oklahoma: Beaver, Beckham, Bryan, Caddo, Choctaw, Cleveland, Creek, Grady, Haskell, Kingfisher, McClain, Major, Muskogee, Oklahoma, Osage, Payne, Pittsburg, Pottawatomie, Tulsa, and Washington counties.

pennsylvania: Bedford, Berks, Delaware, Fulton, Lebanon, and Luzerne counties.

rhode island: Kent and Providence counties.

south carolina: Aiken, Allendale, Anderson, Berkeley, Darlington, Marion, Oconee, and Pickens counties.

tennessee: Grundy, Hamilton, Knox, and McNairy counties.

texas: Anderson, Austin, Bastrop, Bowie, Caldwell, Dallas, Houston, Leon, Milam, Montgomery, Smith, Wilson, and Wood counties.

vermont: Chittenden County.

virginia: Bedford, Fairfax, Henrico, James City, Louisa, and Southampton counties.

west virginia: Fayette, Hampshire, and Hardy counties.

wisconsin: Adams, Columbia, Crawford, Dane, Eau Claire, Grant, Green, Iowa, Juneau, Marquette, Racine, Rock, Waupaca, Waushara, and Wood counties.

Asclepias amplexicaulis is one of the most infallibly recognizable species of the genus. Nevertheless, it has occasional deviations of floral structure, although of a sporadic nature. In Florida it seems to hybridize occasionally with *A. humistrata,* a somewhat similar appearing plant of similar environments although I have placed the latter in a different series (SYRIACAE).

27. ASCLEPIAS VIRLETII Fourn. in Ann. Sci. Nat. Ser. VI, 14:378. 1882, ex char. [T.: *Virlet 1685.*]

Asclepias longipedunculata Brandg. in Univ. Calif. Publ. Bot. 4:277. 1912. [T.: *Purpus 5219,* MO!]

More or less decumbent, subscapose perennials from a fleshy, napiform rootstalk. Stems slender, simple or branching sparingly from the base, erect or decumbent, 1–3 dm. tall, minutely appressed-puberulent. Leaves opposite, broadly oval to oblong-lanceolate, apex obtuse to acute, base broadly obtuse or rounded, 3–5 cm. long, 1–2 cm. broad, firmly membranaceous, minutely and generally puberulent particularly below; petioles 5 mm. long to obsolete. Inflorescences subterminal and solitary from one of the upper nodes, several-flowered; peduncles rather stout, 9–18 cm. long, minutely puberulent; pedicels slender, 1–2 cm. long. Flowers moderately large; calyx lobes lance-trigonal, about 2 mm. long, minutely puberulent-papillate; corolla reflexed-rotate, livid purple or red, the lobes 6–8 cm. long; gynostegium cream or pale purplish or rose, shortly stipitate, the column obconic, 2.0–2.5 mm. long, 2–3 mm. broad, the hoods tubular-cucullate, erose-dentate, about 3–4 mm. long, the horn almost wholly adnate, somewhat longer than the hood, entire at the tip, ascending, the anther head rather broadly cylindrical, about 2 mm. long and 2–3 mm. broad. Follicles erect on deflexed pedicels, narrowly fusiform, 8–12 cm. long, 6–8 mm. thick, smooth, densely and minutely puberulent; seeds oval, about 5 mm. long, the white coma about 3.5 cm. long.

Open woods in canyons and calcite or limestone hills. Northeastern Mexico. Blooming from May to July.

MEXICO: NUEVO LEON: Galeana, Pablillo, Potosí Mountain. PUEBLA: Puebla. SAN LUIS POTOSÍ: Bagre.

Rather doubtfully distinct from *A. scaposa.* Besides the larger flowers and more caulescent plants, this species (if it is such!) has peculiar dentate corona horns, and it is upon the basis of this unusual character that I am interpreting Fournier's species, the types of which apparently have been lost or misplaced in the Paris Herbarium.

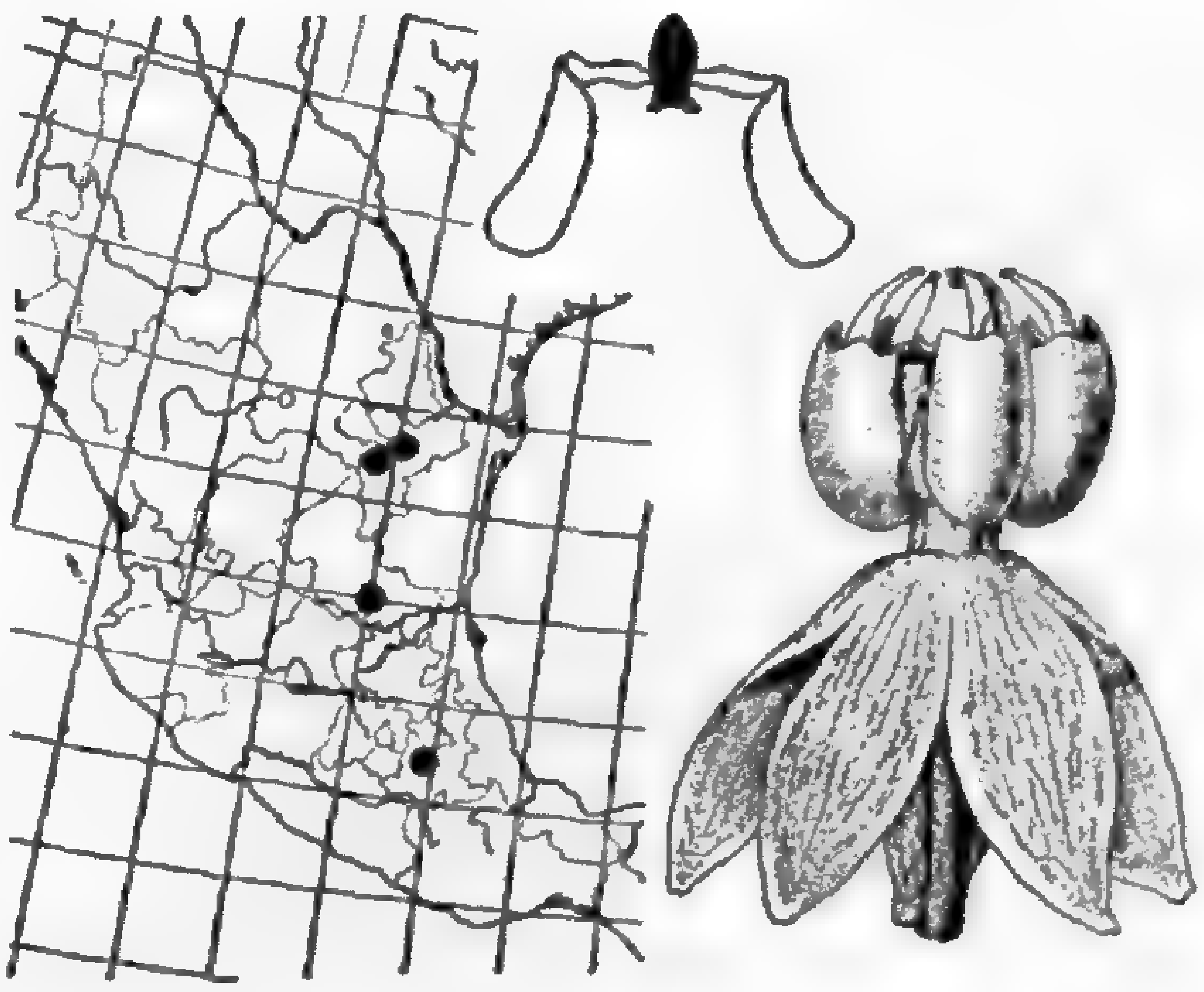

Fig. 33. *Asclepias virletii* Fourn.

28. **Asclepias scaposa** Vail, in Bull. Torrey Bot. Club 25:171. 1898. [T.: *Wright 7,* MO!]

Asclepias exilis M. E. Jones, Contr. West. Bot. 12:48. 1908. [T.: *Jones 568,* MO!]
Asclepias rafaelensis Brandg. in Univ. Calif. Publ. Bot. 4:277. 1912. [T.: *Purpus 5214,* MO!]

Small, subscapose herbaceous perennials from a fleshy napiform rootstalk. Stems simple or sparingly branched from the base, slender, 5–12 cm. tall, minutely and generally puberulent or pilosulose. Leaves opposite, petiolate, broadly oval to oblong-elliptic, apex obtuse to acute, base obtuse to rounded, 2–6 cm. long, 0.5–2.5 cm. broad, membranaceous, generally pilosulose above and below; petioles 0.5–4.0 cm. long. Inflorescences terminal, solitary, several- to many-flowered; peduncle relatively stout, 7–17 cm. long; pedicels slender, 1–2 cm. long. Flowers rather small; calyx lobes lance-trigonal, about 2 mm. long, minutely pilosulose; corolla reflexed-rotate, livid rose or purplish, the lobes 4–5 mm. long; gynostegium shortly stipitate, cream flushed with purple or rose, the column obconic, 1.0–1.5 mm. long and broad, the hoods tubular-cucullate, erose-dentate, 2–3 mm. long, the horn acicular and ascending, somewhat longer than the hood and strongly adnate to it, entire, the anther head about 1.5 mm. long and 2 mm. broad. Follicles erect on deflexed pedicels, narrowly fusiform, about 5 cm. long and 5–7 mm. thick, smooth, minutely pilosulose; seeds unknown.

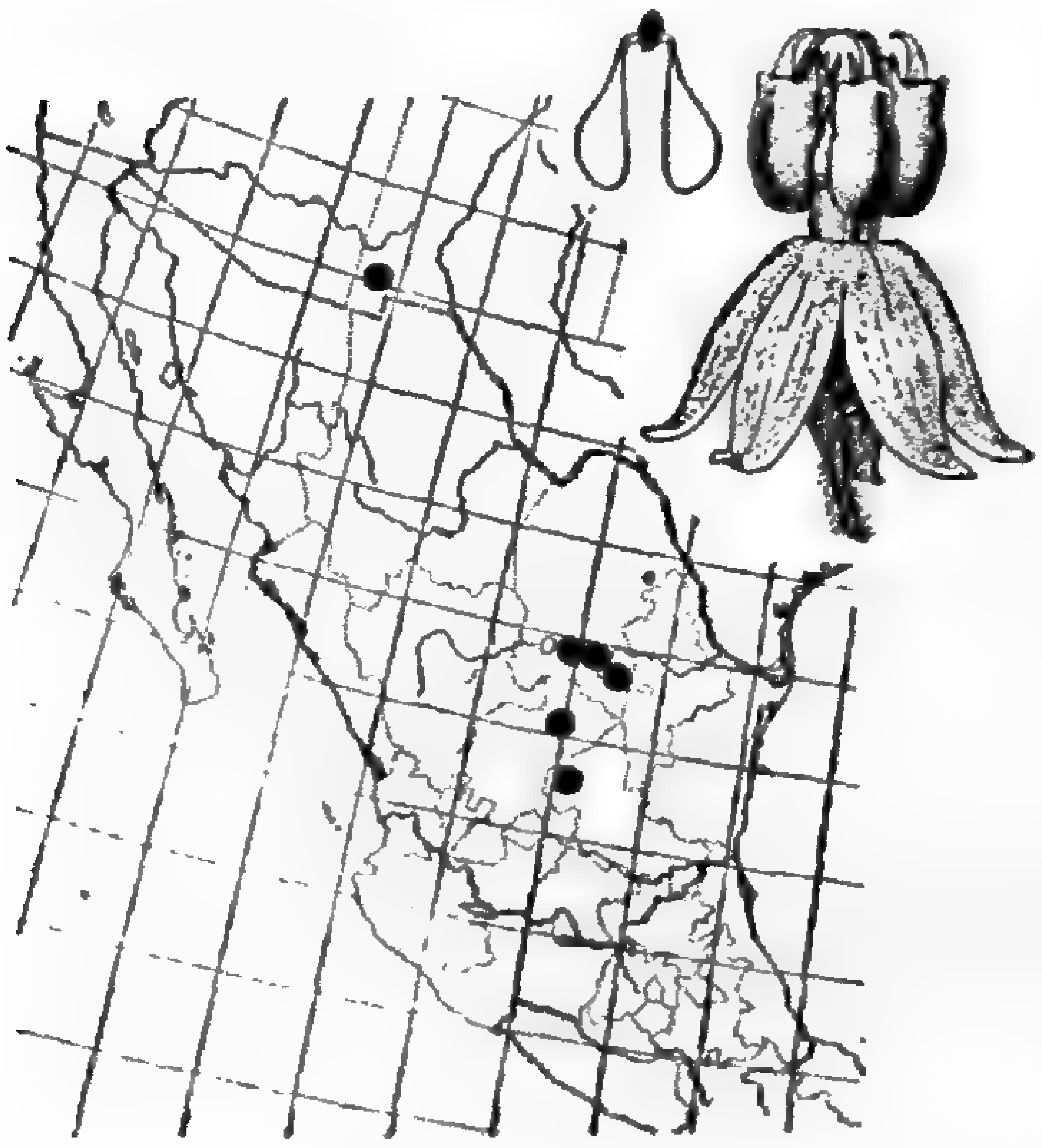

Fig. 34. *Asclepias scaposa* Vail

Dry, sunny, gravelly openings among scrub oaks, mountain sides and flats. Southern New Mexico; north-central Mexico. Flowering from March to October.

United States:
new mexico: Grant County (?).
Mexico: coahuila: Saltillo, La Noria, Sierra de Parras. san luis potosí: Minas de San Rafael. zacatecas: Pastorilla.

Asclepias scaposa has been rather an enigma since its description from a single depauperate fruiting specimen by Miss Vail in 1898. This, which remains the only specimen recorded from the United States as well as the only fruiting specimen of the species, was found duplicated in both the Gray Herbarium and the herbarium of the New York Botanical Garden without a number; in the herbarium of the Missouri Botanical Garden a third duplicate bears the number 7, which probably is an arbitrary number assigned by Engelmann and not a field number in the true sense. Without a field number, the actual place of collection of Wright's specimen cannot be ascertained; it appears more than possible that it may have been actually in Coahuila, considerably south of the present boundary of New Mexico.

Asclepias scaposa is very closely related to *A. virletii,* differing chiefly in the truly terminal inflorescences and the smaller flowers (together with such technical characters of the hoods as the entire, acicular horns). I do not believe these features to be environmental, however, since they are fairly constant; Runyon (*sub 1326* in U. S. Nat. Herb.) collected unusually lush specimens in "black fertile soil" near Saltillo, but they still produced the solitary terminal inflorescences and small flowers.

Series 4. GRANDIFLORAE

KEY TO THE SPECIES

a. Leaves shortly but definitely petiolate, acute to obtuse at the base; peduncles much shortér than the subtending leaves; flowers relatively large, the corolla lobes spreading or somewhat ascending, about 1.5 cm. long; column cylindric, about as long as broad; hoods rather narrow, acuminate. Southwestern Jalisco ....29. *A. crocea*

aa. Leaves sessile, deeply cordate and amplexicaul; peduncles usually about as long as the subtending leaves or somewhat longer; column rather broadly obconic to essentially obsolete; hoods about as broad as long.

  b. Flowers relatively large, the corolla lobes spreading or somewhat ascending, 1.5–2.0 cm. long; hoods 6–11 mm. long, broadly acute. Mexico southward to Oaxaca....30. *A. grandiflora*

  bb. Flowers relatively small, the corolla lobes reflexed, 8–12 mm. long; hoods 5–7 mm. long, broadly rounded or emarginate. Jalisco to Veracruz and southward to Chiapas; Guatemala; El Salvador; Costa Rica ....31. *A. glaucescens*

29. ASCLEPIAS **crocea** Woodson, spec. nov.

Herbae perennes e caudice elongato subtuberoso. Caules graciliusculi simplices glabri vel juventate inconspicue pilosuli ca 7 dm. alti. Folia opposita petiolata lamina elliptica apice acuminata basi acuta vel obtusa 7–10 cm. longa 1.5–3.5 cm. lata tenuiter membranacea glabra vel subtus tenuissime pilosula et glauca. Inflorescentiae paucae e nodis subterminalibus pauciflores; pedunculis 1–2 cm. longis graciliusculis; pedicellis gracilibus 1.5–2.0 cm. longis pedunculo similibus inconspicue pilosulis. Flores magni speciosissimi; calyci laciniis anguste lanceolatis ca.

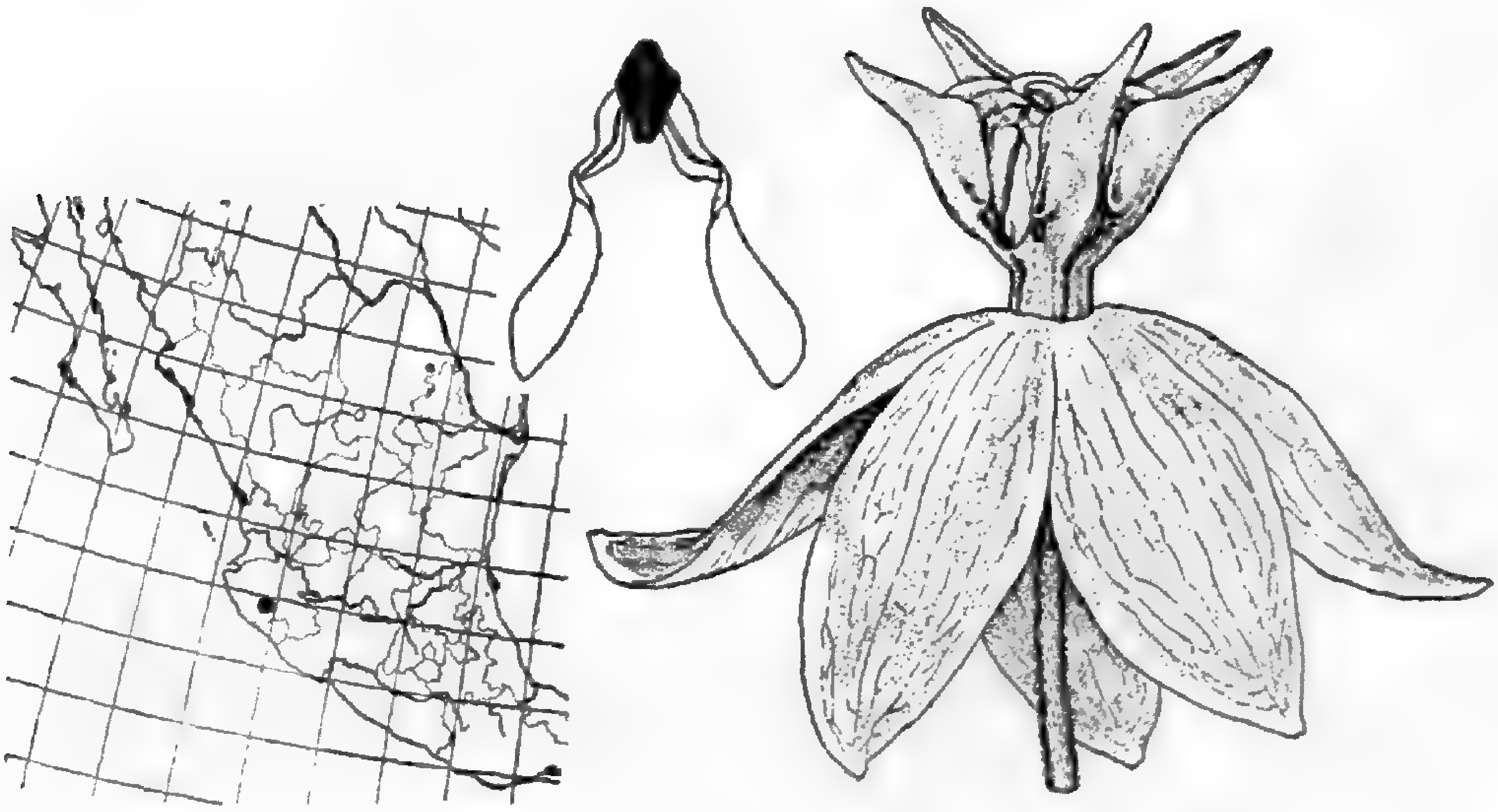

Fig. 35. *Asclepias crocea* Woods.

6 mm. longis sparse pilosulis; corolla rotata pallide crocea extus plus minus fulvotincta, lobis late ellipticis ca. 1.5 cm. longis patulis; gynostegio valde stipitato fulvo, columna late cylindrica ca. 1.5 mm. longa 2.0 mm. lata, cucullis valde conduplicatis rhomboideis acuminatis marginibus acutis breviter stipitatis ca. 7 mm. longis cornu valde adnato incurvato cucullo paullo breviori, androecio late subcylindrico ca. 4 mm. longo et lato. Folliculi ignoti.—HOLOTYPUS: *R. L. & C. R. Wilbur 1990* in Herb. Missouri Bot. Gard. ("Open pine-covered ridges and slopes in mountains e. of Mamantlán about 15 miles south-southeast of Autlán by way of Chante, Jalisco, Mexico, 8700 ft., July 30, 1949.")

Only four plants were found by the collectors at the type locality, but a short distance ("over two hours by hard hiking") away an additional plant was found in bud (*Wilbur & Wilbur 1903* in Herb. Univ. Michigan). Still a third collection has more recently been found in the same vicinity, *McVaugh 13858*, in Herb. Univ. Michigan.

Asclepias crocea was mistaken for *A. grandiflora* at first glance, but is abundantly distinct, as the Key to Species shows.

30. **Asclepias grandiflora** Fourn. in Ann. Sci. Nat. Ser. VI, 14:379. 1882. [T.: *Hahn s. n.*, P!]

Asclepiodora insignis Brandg. in Zoe 5:253. 1908. [T.: *Purpus 2624*, MO!]
Asclepias insignis (Brandg.) Woodson, in Ann. Missouri Bot. Gard. 28:207. 1941.

Herbaceous, glabrous, and extremely glaucous perennials from deep subtuberous rootstalks. Stems stout, simple, 1.5–7.0 dm. tall. Leaves opposite, sessile, very broadly ovate to ovate-oblong, apex very broadly obtuse to rounded and usually mucronulate, base broadly cordate and amplexicaul, 5–12 cm. long, 1.5–6.0 cm. broad, usually rather strongly crispate and apparently somewhat succulent. Inflorescences solitary and lateral at the upper several nodes, sometimes subterminal,

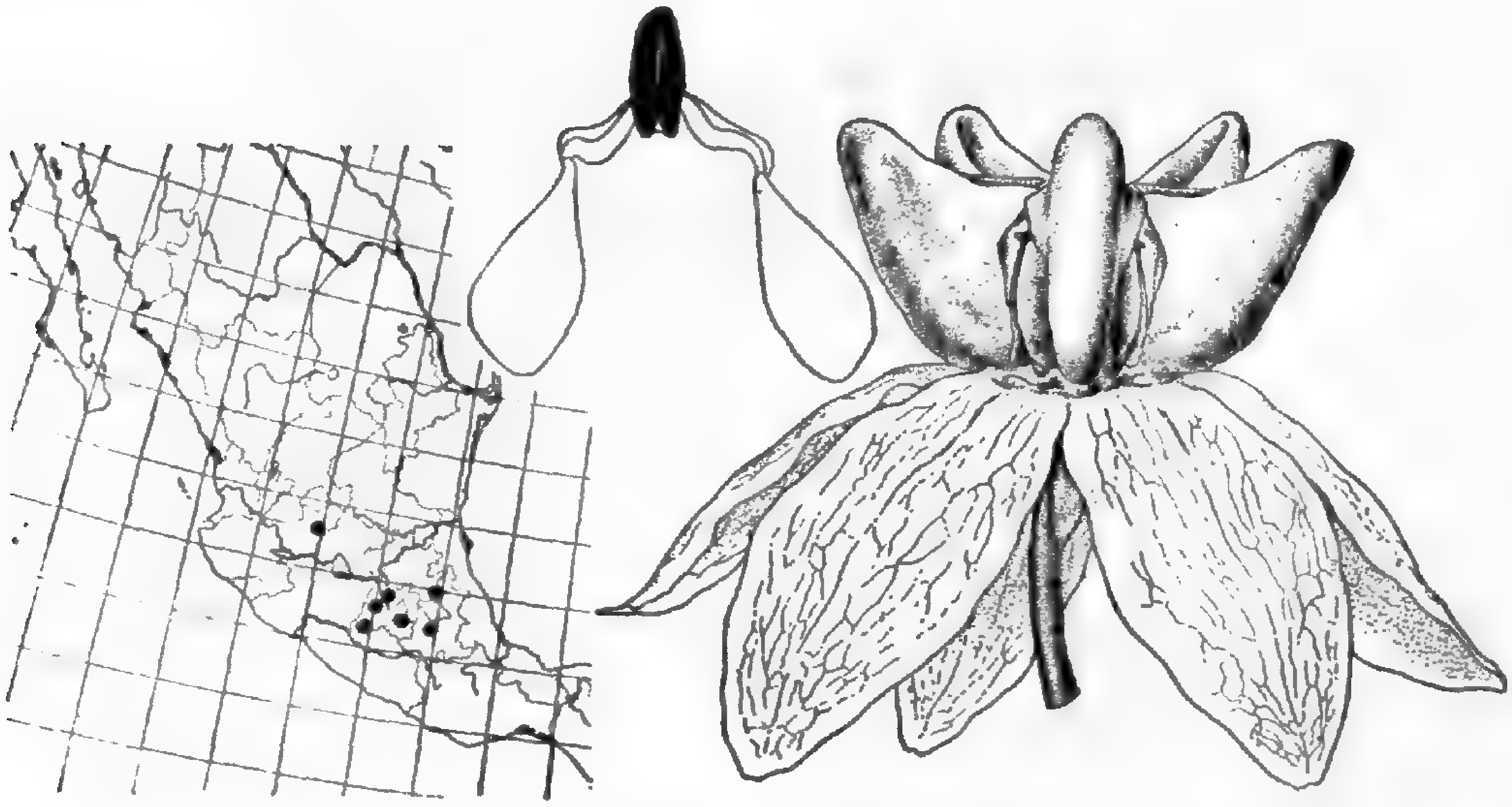

Fig. 36. *Asclepias grandiflora* Fourn.

rather few-flowered; peduncles rather stout, 4–8 cm. long; pedicels rather slender, 1–3 cm. long. Flowers very large and showy; calyx lobes ovate, 6–8 mm. long, glaucous and suffused with purple; corolla rotate, pale green, usually rather strongly suffused with purple without, the lobes 1.5–2.0 cm. long, spreading or somewhat ascending; gynostegium rather broadly stipitate, apparently greenish cream with the keel somewhat suffused with purple or brown, the column obconic, 4–5 mm. long and broad, the hoods strongly conduplicate, broadly hastate-rhombic, obtuse at the apex, the marginal lobes acute and recurved, shortly stipitate, 6–11 mm. long, the horn short and incurved or reduced to a rather low crest, the anther head 4–5 mm. long and broad. Follicles erect on deflexed pedicels, narrowly fusiform, 8–12 cm. long, about 1.0–1.5 cm. thick, smooth, very minutely and scatteringly puberulent to glabrate; seeds broadly oval, about 6 mm. long, the pale yellowish or white coma about 3.5 cm. long.

Hillsides, frequently in open oak woods. Southeast-central Mexico. Blooming from July to October.

MEXICO: GUERRERO: Taxco, Limón Mt. JALISCO: Huejuquilla. MEXICO: Temascaltepec. MORELOS: Cuantla, Xochiltepec. PUEBLA: Tlacuiloltepec, San Luis Tultitlanapa.

This is one of the showiest American asclepiads, rivalling the best of the South African species. A popular name reported by Hinton is *lechetresna,* which is also applied to *A. contrayerba* and other species.

31. ASCLEPIAS GLAUCESCENS HBK. Nov. Gen. 3:190. *t. 227.* 1819. [T.: *Bonpland 3920,* MO, photo!]

Asclepias glaberrima Sessé & Moc. La Naturaleza ser. 2, 1:app. 43. 1888. [T.: *Sessé & Moc. 1278,* F!]
Asclepias polyphylla Brandg. in Univ. Calif. Publ. Bot. 6:371. 1917. [T.: *Purpus s. n.,* MO!]

Herbaceous, glabrous, and glaucous perennials from rather deep fleshy rootstalks. Stems rather stout, simple, 1.5–8.0 dm. tall. Leaves opposite, sessile, broadly ovate or oval to narrowly ovate-oblong, apex broadly acute to rounded, frequently mucronulate, base broadly cordate and amplexicaul, frequently rather crispate and apparently somewhat succulent, 6–18 cm. long, 1–7 cm. broad. Inflorescences solitary and lateral at few or several of the upper nodes, occasionally solitary and terminal, several- to many-flowered; peduncles rather stout, 2–20 cm. long; pedicels rather stout, 1.0–3.5 cm. long. Flowers rather large; calyx lobes ovate-lanceolate, 4–5 mm. long; corolla reflexed-rotate, greenish cream frequently suffused with rose or purple without, the lobes 8–12 mm. long; gynostegium shortly stipitate to subsessile, cream or pinkish, the column broadly cylindrical, about 1 mm. long and 2 mm. broad, the hoods strongly conduplicate, obovate, rounded and frequently emarginate, the marginal lobes broadly obtuse or rounded, 5–7 mm. long, the horn almost wholly adnate, rather short and incurved, the anther head shortly cylindrical, about 3 mm. long and 3–4 mm. broad. Follicles erect on deflexed pedicels, narrowly fusiform, 8–10 cm. long and about 1 cm. thick, smooth,

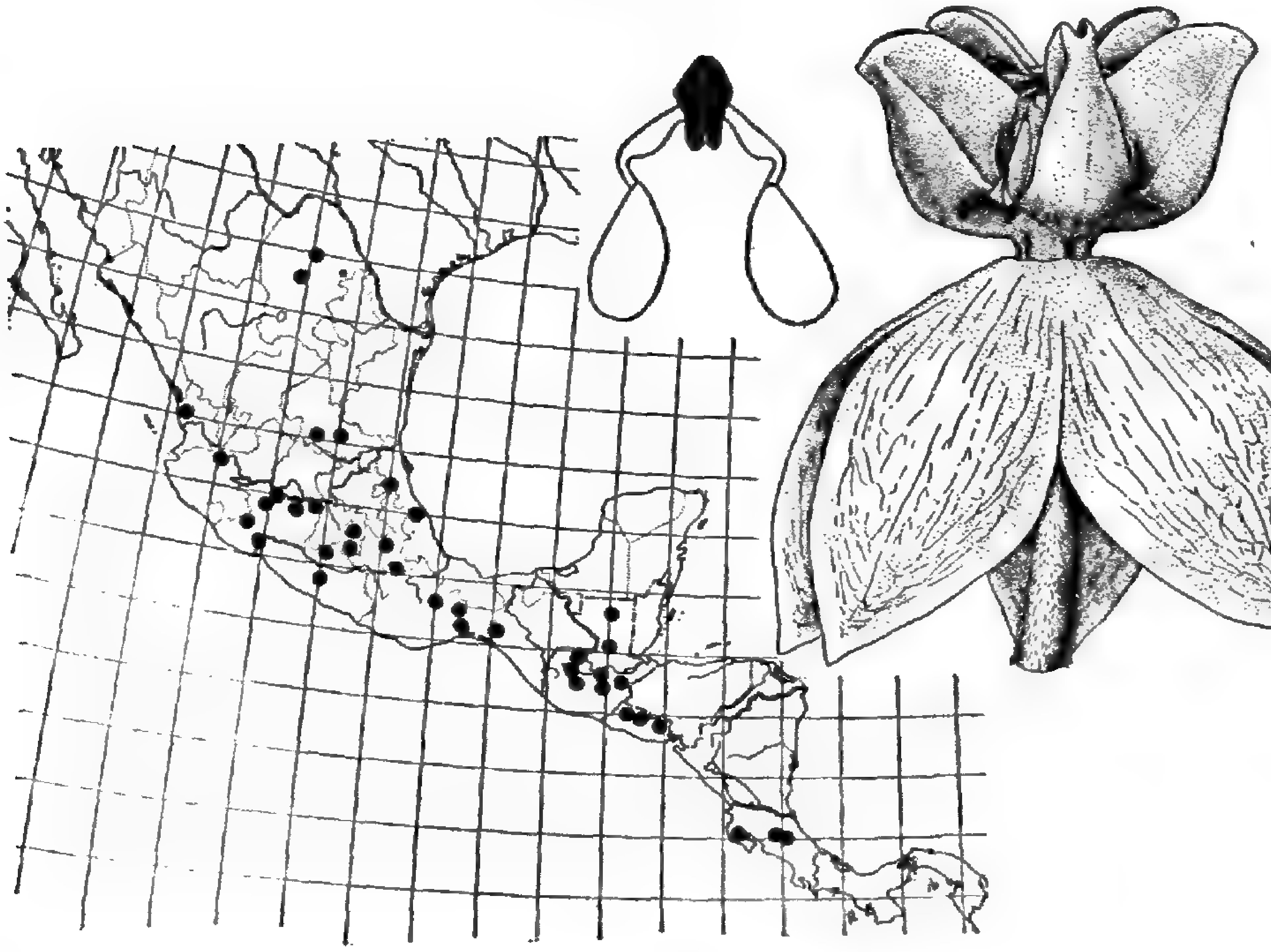

Fig. 37. *Asclepias glaucescens* HBK.

glabrous; seeds broadly oval, 6–8 mm. long, the white coma 2.5–3.5 cm. long.

Open oak-pine woods, grassy hills and llanos, spreading to dry fields and roadsides. Central Mexico to Guatemala, El Salvador, and Costa Rica.

MEXICO: CHIAPAS: Cerro de Tonalá. COAHUILA: Múzquiz, Parras. GUERRERO: Chilpancingo, Coyuca, Taxco. JALISCO: San Marcos. MEXICO: Temascaltepec. MICHOACAN: Apatzingán, Volcán Jorullo, Los Reyes, Hacienda Coahuayutla, Zinapecuaro, Coalcomán. MORELOS: Yautepec, Cuernavaca, Valle del Tepeite, Tepoztlán. NAYARIT: Tepic. OAXACA: Tehuantepec, San Pedro Yolox, San Luis, Yalalag, Cerro de San Felipe. PUEBLA: Atlixco, Cerro de Gavilán. SAN LUIS POTOSÍ: San Luis Potosí, Las Canoas. VERACRUZ: San Martin Tlactopec, Maltrata.

GUATEMALA: ALTA VERAPAZ: Sacanquim, Sepacuite, Lanquin. CHIMALTENANGO: Chimaltenango, San Martín Jilotepeque. CHIQUIMULA: Río Tacó. GUATEMALA: Guatemala. HUEHUETENANGO: Río Pucal, San Rafael Pétzal, Los Pinitos, Huehuetenango, San Sebastián H., Democracia. JALAPA: Río Jalapa. PETÉN: La Libertad. SOLOLÁ: San Pedro.

EL SALVADOR: SAN SALVADOR: Cerro de San Jacinto, San Salvador, San Martín, Laguna de Iloponga. SAN VICENTE: San Vicente.

COSTA RICA: ALAJUELA: Circeles. CARTAGO: Las Cóncavas, La Carpintera. SAN JOSÉ: Tres Ríos.

Popular names reported for *A. glaucescens* are *lechetresma* (Mexico), *oreja de liebre* (Veracruz), *capuyo leche, polín,* and *jicaca* (Guatemala and El Salvador), and *mata coyote* (El Salvador). The plant is reputed to be poisonous, but is used in the treatment of colic and to bring boils to a head.

A discussion of the relationship of *A. glaucescens* and *A. elata* will be found under the latter species.

Series 5. SYRIACAE

KEY TO THE SPECIES

a. Plants herbaceous; leaves opposite.

b. Hoods sessile or subsessile and more or less pouched at the base.

c. Hoods broadly rounded to broadly acute at the tip; horn typically present.

d. Hoods delicately petalaceous; glands of translators relatively minute; follicles erect on erect pedicels.

e. Leaves ovate-elliptic, two or rarely three nodes typically condensed to form a false whorl; corolla pale pink. Southeastern Ontario; Massachusetts to Virginia and westward to Kansas and Oklahoma ....32. *A. quadrifolia*

ee. Leaves linear to filiform, opposite; corolla greenish white more or less suffused with purple. Northern Florida ....33. *A. viridula*

dd. Hoods fleshy and more or less inflated; glands of translators relatively massive.

e. Plants generally puberulent or tomentulose; leaves definitely petiolaté.

f. Hoods about as long as the anther head; corolla dull rose, occasionally white; follicles pendulous or subpendulous, the seeds naked. Southern San Luis Potosí to northern Guatemala ....34. *A. pellucida*

ff. Hoods twice as long as the anther head or nearly so; follicles erect on deflexed pedicels.

g. Plants relatively slender; leaves 3–7 cm. long; flowers relatively few and lax; corolla greenish white tinged with purple, the lobes about as long as the hoods; follicles smooth. Wisconsin and northern Illinois to the Dakotas; southern Manitoba to Saskatchewan ....35. *A. ovalifolia*

gg. Plants relatively stout; leaves 6–30 cm. long or more; flowers very many and crowded; corolla dull purplish rose (rarely white), the lobes longer than the hoods; follicles softly spinose (rarely smooth). New Brunswick to Virginia and westward to North Dakota and Kansas; locally introduced elsewhere in the United States ....36. *A. syriaca*

ee. Plants essentially glabrous; leaves sessile or subsessile.

f. Plants prostrate or decumbent; leaves deeply cordate, sessile and amplexicaul; flowers rather small and numerous; corolla pale pink. Coastal Plain: North Carolina to Louisiana ....37. *A. humistrata*

ff. Plants erect; leaves obtuse or broadly rounded at the base; flowers moderately large and few; corolla greenish cream tinged with purple. Southern Wisconsin and northern Illinois westward to Iowa and eastern Kansas........38. *A. meadii*

cc. Hoods narrowly but obtusely acuminate, deep purple; horn typically absent; corolla pale green suffused with purple. Southern New Mexico and Arizona; northern Chihuahua and Sonora ....39. *A. hypoleuca*

bb. Hoods distinctly stipitate, flattened dorsally, not pouched at the base; corolla greenish white tinged with purple without.

c. Plants softly puberulent generally; stems relatively stout; leaves broadly ovate, moderately large; flowers small and very crowded; body of the hood scarcely longer than the stipe; horn frequently absent; follicles pendulous, the seeds naked. Jalisco and southern San Luis Potosí southward to Morelos and Puebla........40. *A. pringlei*

cc. Plants essentially glabrous; stems rather slender; leaves lanceolate to ovate-lanceolate, rather small; flowers rather few and lax; body of the hood much longer than the stipe; horn typically present; follicles erect on deflexed pedicels, the seeds comose. Sinaloa to Michoacan ....41. *A. pratensis*

aa. Plants fruticose to suffruticose; leaves spirally approximate, filiform, pine-like; flowers rather small and crowded, greenish white. Southern Arizona and adjacent California; southward virtually throughout highland Mexico to Oaxaca........42. *A. linaria*

Asclepias quadrifolia and *A. viridula* are placed in series SYRIACAE with considerable misgivings: because of the follicles erect on erect pedicels I would much rather place them with the INCARNATAE, as well as because of the petalaceous coronas. However, in other respects the floral structure is similar to the more typical species of the series, and these species might be considered as indicating the origin of the SYRIACAE from the INCARNATAE.

Asclepias hypoleuca, similarly, seems to show a transition to the MACROTIDES because of the apparently somewhat keeled hoods; and *A. humilis*, *A. pratensis*, and *A. linaria* transitions to the PURPURASCENTES because the hoods are flattened dorsally. All are maintained in SYRIACAE because of the pronounced marginal lobes of the hoods.

32. ASCLEPIAS QUADRIFOLIA Jacq. Obs. Bot. 2:8. 1767, ex char.

Asclepias vanillea Raf. in Amer. Monthly Mag. 4:39. 1818, ex char.
Asclepias quadrifolia var. *oppositifolia* Raf. Aut. Bot. 177. 1840, ex char.

Herbaceous perennials from rather long and fleshy rootstalks. Stems slender, 2–5 dm. tall, usually simple, more or less puberulent in decurrent lines from the nodes. Leaves basically opposite but two (or rarely three) nodes usually condensed to form a false whorl, petiolate or the lowermost sessile or subsessile, ovate to ovate-elliptic, acuminate, the base obtuse or rounded and usually somewhat decurrent, 2.5–12.0 cm. long, 1–6 cm. broad, thinly membranaceous, glabrous or very indistinctly pilosulose beneath; petioles 0.5–2.5 cm. long or nearly obsolete. Inflorescences terminal and solitary, occasionally lateral also at the uppermost node, several- to many-flowered; peduncles 1.5–3.5 cm. long, slender, inconspicuously pilosulose; pedicels 1.5–3.0 cm. long, pilosulose. Flowers rather small; calyx lobes lanceolate, about 1.5 mm. long; corolla reflexed-rotate, pale pink or cream, the lobes about 5 mm. long; gynostegium shortly stipitate, white, the column broadly obconic, about 1 mm. long and 1.0–1.5 mm. broad, the hoods cucullate, 4–5 mm. long, somewhat spreading, obtuse or rounded at the tip, with very pronounced marginal lobules and more or less conspicuous, excurrent lateral appendages at the base, the horn basally adnate, rather broadly acicular, somewhat longer than the

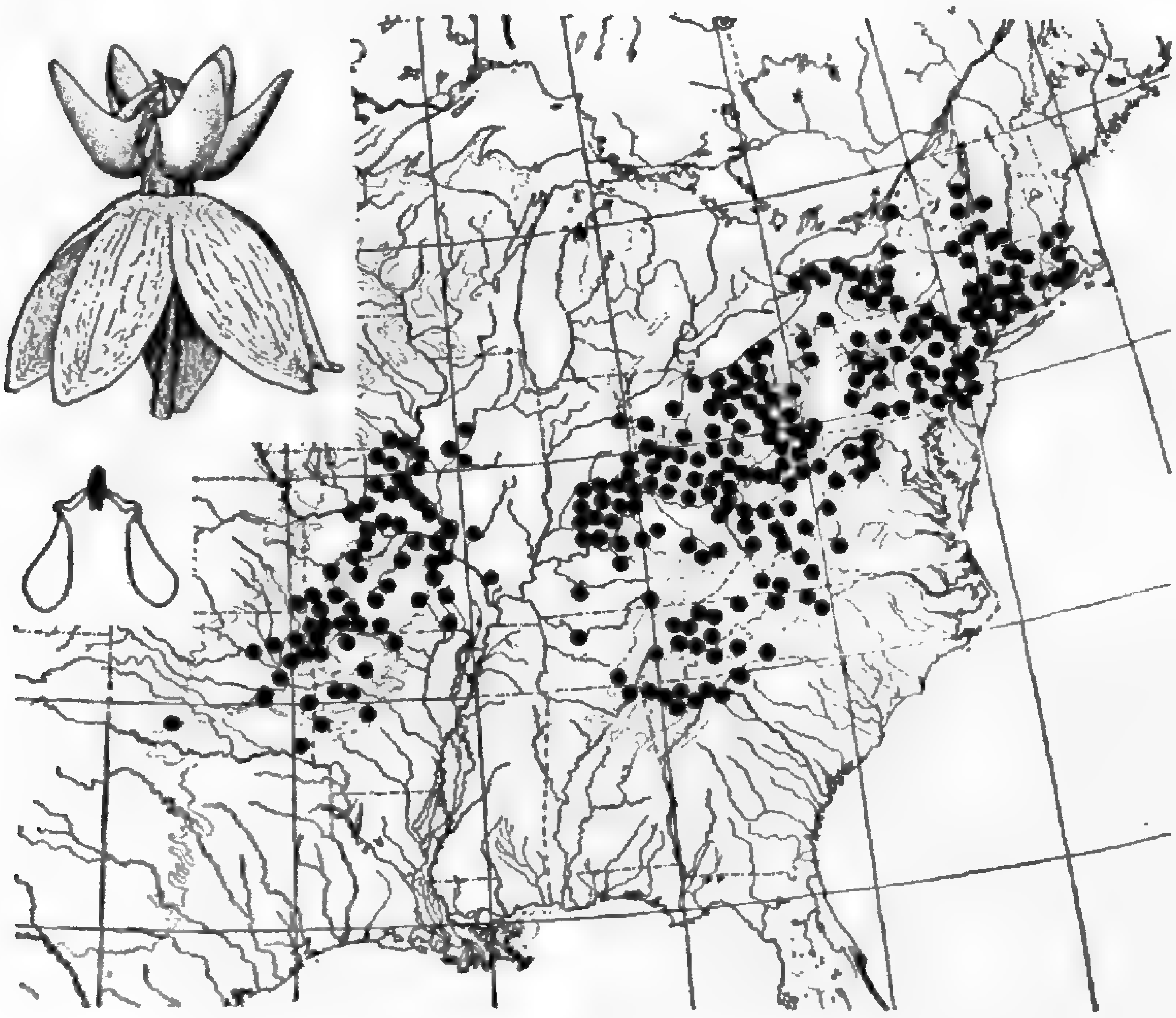

Fig. 38. *Asclepias quadrifolia* Jacq.

hood, incurved toward the anther head, the anther head broadly truncate-conic, about 2 mm. long and 2.5 mm. broad. Follicles erect on erect pedicels, narrowly fusiform, 8–12 cm. long, about 4–8 mm. thick, smooth, glabrous; seeds oval, about 7 mm. long, the white or pale tawny coma about 3.5 cm. long.

Woods and thickets, usually rather dry and rocky. Southwestern Vermont to northeastern Alabama and westward to southeastern Indiana; Iowa, Arkansas, and adjacent Illinois, Oklahoma, and Kansas; Canada (southeastern Ontario). Flowering from April until July.

CANADA: ONTARIO: Welland County.

UNITED STATES:

ALABAMA: Jackson County.

ARKANSAS: Benton, Carroll, Conway, Garland, Izard, Logan, Polk, Washington, and Yell counties.

CONNECTICUT: Fairfield, Hartford, Litchfield, Middlesex, New Haven, and Windham counties.

GEORGIA: Dade, Dawson, Gilmer, Lumpkin, Pickens, Walker, and White counties.

IOWA: Lee and Van Buren counties.

ILLINOIS: Adams, Fulton, Greene, Hancock, Peoria, Tazewell, and Union counties.

INDIANA: Bartholomew, Brown, Clark, Crawford, Dearborn, Decatur, Franklin, Harrison, Jackson, Jefferson, Jennings, Lawrence, Monroe, Orange, Ripley, Scott, Switzerland, Washington, and Wells counties.

KANSAS: Cherokee County.

KENTUCKY: Boyd, Breathitt, Fayette, Jefferson, Jessamine, McCreary, Magoffin, Nelson, Warren, Wolfe, and Woodford counties.

MASSACHUSETTS: Berkshire, Bristol, Essex, Franklin, Hampden, Middlesex, Norfolk, Suffolk, and Worcester counties.

MISSOURI: Barry, Benton, Boone, Callaway, Chariton, Christian, Cooper, Franklin, Gasconade, Greene, Iron, Jasper, Jefferson, Knox, Laclede, Lawrence, Lincoln, McDonald, Macon, Maries, Marion, Monroe, Newton, Ozark, Pettis, Pike, Polk, Ralls, Ripley, St. Francois, St. Louis, Saline, Schuyler, Scotland, Shannon, Stone, Taney, Texas, and Wayne counties.

NEW JERSEY: Bergen, Burlington, Gloucester, Hunterdon, Mercer, and Somerset counties.

NEW YORK: Albany, Allegheny, Cayuga, Columbia, Dutchess, Essex, Genesee, Greene, Jefferson, Monroe, Niagara, Onondaga, Ontario, Orange, Rensselaer, Rockland, Saratoga, Schoharie, Schuyler, Seneca, Tioga, Tompkins, Ulster, Warren, Washington, Westchester, and Yates counties.

NORTH CAROLINA: Ashe, Buncombe, Guilford, Haywood, Polk, and Stokes counties.

OHIO: Adams, Ashtabula, Auglaize, Belmont, Carroll, Clark, Clermont, Clinton, Columbiana, Cuyahoga, Delaware, Erie, Fairfield, Gallia, Greene, Hamilton, Highland, Hocking, Jackson, Knox, Lake, Lawrence, Lorain, Madison, Medina, Meigs, Miami, Monroe, Montgomery, Perry, Pickaway, Pike, Portage, Richland, Ross, Scioto, Stark, Summit, Tuscarawa, Warren, Wayne, and Wyandot counties.

OKLAHOMA: Adair, Cherokee, Comanche, Delaware, Le Flore, McCurtain, Mayes, Muskogee, and Tulsa counties.

PENNSYLVANIA: Bedford, Berks, Bradford, Bucks, Centre, Chester, Clarion, Clinton, Delaware, Fayette, Franklin, Fulton, Greene, Huntingdon, Juniata, Lackawanna, Lancaster, Lebanon, Lehigh, Luzerne, Lycoming, Mifflin, Monroe, Montgomery, Northampton, Pike, Schuylkill, Snyder, Warren, Washington, Wayne, Wyoming, and York counties.

RHODE ISLAND: Providence County.

SOUTH CAROLINA: Pickens County.

TENNESSEE: Anderson, Blount, Davidson, Franklin, Grainger, Knox, Loudon, Rhea, Sevier, Sullivan, and Union counties.

VERMONT: Bennington, Rutland, and Windham counties.

VIRGINIA: Bath, Bedford, Clarke, Giles, Grayson, Montgomery, Smyth, Shenandoah, and Warren counties.

WEST VIRGINIA: Berkeley, Braxton, Cabell, Calhoun, Greenbier, Hampshire, Kanawha, Lincoln, Marion, Mingo, Monongalia, Nichols, Pendelton, Polk, Raleigh, Randolph, Summers, Upshur, Wayne, Wetzel, and Wirt counties.

This charming little species is remarkably constant in spite of the sporadic failure of its nodes to form the characteristic false whorl. It is rather odd that its two disjunct populations have not evolved morphological differentiation of some sort.

33. ASCLEPIAS VIRIDULA Chapm. Fl. Southern U. S. 363. 1860. [T.: *Chapman s.n.*, MO!]

Herbaceous perennials from rather long fleshy rootstalks. Stems solitary or occasionally in small clusters, slender, simple, glabrous or minutely pilosulose in lines decurrent from the nodes, 3–4 dm. tall. Leaves opposite, sessile, linear to filiform, 2–7 cm. long, 1–2 mm. broad, membranaceous, glabrous. Inflorescences terminal and lateral at a few of the uppermost nodes, several-flowered; peduncles 0.5–3.0 cm. long, slender; pedicels very slender, about 1 cm. long. Flowers rather small; calyx lobes ovate, 2.0–2.5 mm. long; corolla reflexed-rotate, pale purplish green, the lobes about 5 mm. long; gynostegium shortly stipitate, white, the column obconic, about 1 mm. long and broad, the hoods cucullate, about 3 mm. long, somewhat spreading, rounded at the tip and with conspicuous marginal lobes, the horn falciform, adnate at the base, about as long as the hood, the anther head 1.0 mm. long and about 1.5 mm. broad. Follicles erect on erect pedicels, narrowly fusiform, 8–10 cm. long, about 6 mm. thick, smooth, glabrous; seeds broadly oval, about 8 mm. long, the white coma 2.5–3.0 cm. long.

Fig. 39. *Asclepias viridula* Chapm.

Open flatwoods. Northern Florida. Blooming from April to July.

UNITED STATES:

FLORIDA: Baker, Bradford, Duval, Flagler, Franklin, and Nassau counties.

Perhaps closely related to *A. michauxii* which it resembles in many respects; although the two ranges coincide in Florida, I have observed no intergradation between them.

34. ASCLEPIAS PELLUCIDA Fourn. in Ann. Sci. Nat. Ser. VI, 14:381. 1882. [T.: *Botteri 317*, P!]

Herbaceous perennials. Stems relatively stout, simple, occasionally with weak sterile axillary branches toward the base, 1–4 m. tall, glabrous or inconspicuously pilosulose at the nodes. Leaves opposite, petiolate, broadly ovate- to oblong-elliptic, apex narrowly acuminate, base obtuse to rounded, 7–30 cm. long, 2.5–9.0 cm. broad, thinly membranaceous, glabrous above, weakly pilosulose on the midrib and veins beneath; petioles 2–3 cm. long. Inflorescences lateral and solitary at few or several of the uppermost nodes, several- to many-flowered; peduncles 4–10 cm. long, relatively stout, scatteringly pilosulose; pedicels rather slender, 2–4 cm. long. Flowers rather small; calyx lobes oblong-lanceolate, 3–4 mm. long; corolla dull rose, occasionally white, the lobes 6–8 mm. long; gynostegium shortly stipitate, pale rose to white, the column obconic, about 1 mm. long and 1.5 mm. broad, the hoods cucullate, obovate, 2.5–3.5 mm. long, the horn shortly falciform, about half adnate, somewhat longer than the hood, the anther head truncately conic, 2–3 mm. long, about 3–4 mm. broad. Follicles pendulous on pendulous peduncles, rather broadly ovoid, abruptly apiculate, 7–8 cm. long, 2–4 cm. thick, smooth, glabrous; seeds broadly oval, about 1.5 cm. long, naked.

Fig. 40. *Asclepias pellucida* Fourn.

Pine-oak forests, barrancas. Southern Mexico; Guatemala. Blooming sporadically throughout the year.

MEXICO: CHIAPAS: locality indefinite. GUERRERO: Mina, Sierra Madre. HIDALGO: Trinidad Iron Works. JALISCO: Sierra de Manantlán. MEXICO: Temascaltepec. OAXACA: Dto. Cuicatlan. SAN LUIS POTOSÍ: Alvarez. VERACRUZ: Orizaba.

GUATEMALA: HUEHUETENANGO: Santa Eulalia.

The naked seeds of *A. pellucida* suggest an adaptation for dissemination by water, but the meagre field notes of collectors do not confirm this.

35. **Asclepias ovalifolia** Dcne. in DC. Prodr. 8:567. 1844. [Based on *A. variegata β minor* Hook.]

Asclepias variegata β minor Hook. Fl. Bor.-Amer. 2:52, *t. 141.* 1838, ex ic. [T.: *Richardson s. n.*]

Herbaceous perennials. Stems relatively slender, simple or sometimes branched below ground, 1–3 dm. tall, densely and minutely puberulent. Leaves opposite, shortly petiolate, broadly ovate or oval to rather narrowly elliptic, apex broadly acute to obtuse, base obtuse to rounded, 3–7 cm. long, 1.5–4.0 cm. broad, membranaceous, softly and generally puberulent particularly below; petioles 2–7 mm. long. Inflorescences terminal and solitary occasionally also from the uppermost node, several-flowered; peduncles rather slender, 1–7 cm. long; pedicels slender, 1.5–2.0 cm. long. Flowers rather small; calyx lobes ovate-lanceolate, 3–4 mm. long, densely puberulent; corolla reflexed-rotate, greenish white and somewhat tinged with purple without, the lobes 5–7 mm. long; gynostegium shortly stipitate, greenish white or cream, the column broadly obconic, about 1 mm. long and 2.5 mm. broad, the hoods cucullate, ovate-rhombic, spreading, about 5 mm. long, the horn adnate toward the base, falciform, incurved, about as long as the hood or somewhat shorter, the anther head truncately conic, about 2 mm. long and 3 mm. broad. Follicles erect on deflexed pedicels, narrowly fusiform, 6–8 cm. long, about 1 cm. thick, smooth, densely puberulent; seeds oval, about 4 mm. long, the pale yellowish coma about 2.5 cm. long.

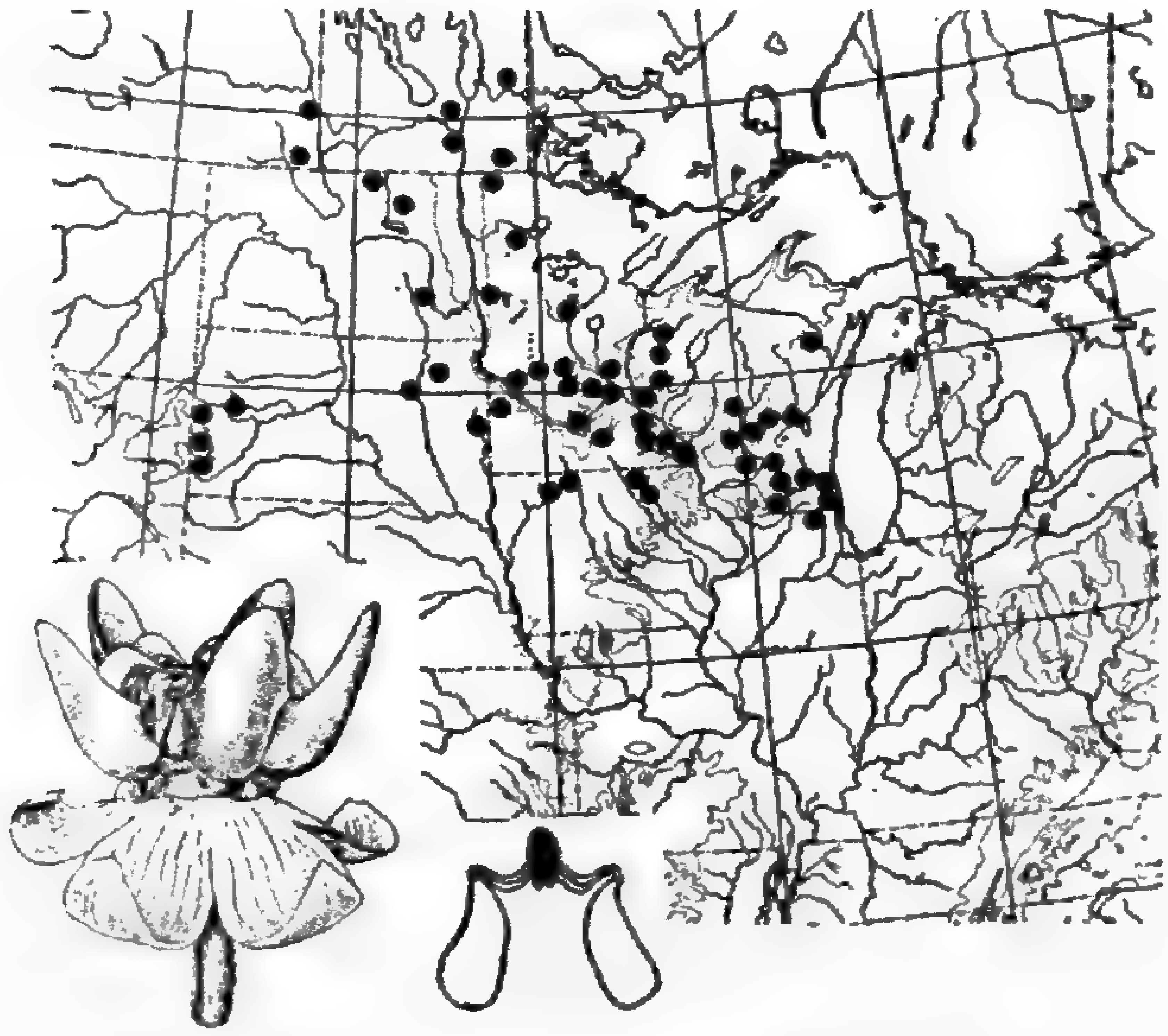

Fig. 41. *Asclepias ovalifolia* Dcne.

Sandy prairies and open woods, gravelly knolls, spreading to railways. Wisconsin and northern Illinois westward to the Dakotas; southern Manitoba and Saskatchewan. Flowering from May to July.

Canada: Manitoba: Birtle, Emerson, Iberville, Killarney, Morris, Norfolk, and St. Clement's counties. Saskatchewan: Canora County.

UNITED STATES:

ILLINOIS: McHenry County.

IOWA: Chickasaw, Clay, Emmet, and Mitchell counties.

MINNESOTA: Anoka, Chippewa, Clay, Clearwater, Crow Wing, Hennepin, Houston, Kandiyohi, McLeod, Meeker, Nicollet, Olmstead, Ramsey, Roseau, Wabasha, Waseca, Winona, and Yellow Medicine counties.

NORTH DAKOTA: Barnes, Benson, and Rolette counties.

SOUTH DAKOTA: Brookings, Custer, Day, Lawrence, Meade, Pennington, and Spink counties.

WISCONSIN: Adams, Barron, Columbia, Dane, Dunn, Jefferson, Juneau, Marinette, Milwaukee, Pierce, Racine, Rock, Sauk, Washburn, Waushara, Winnebago, and Wood counties.

The most characteristic asclepiad of the northern prairies, a charming little species somewhat reminiscent of *A. quadrifolia* in general aspect.

36. ASCLEPIAS SYRIACA L. Sp. Pl. 214. 1753. [T.: Linn. Herb. London, no. *310.14*, photo!]

Asclepias apocinum Gat. Descr. Pl. Montaub. 58. 1789, ex char.
Asclepias pubescens Moench, Meth. 716. 1794, non L., ex char.
Asclepias capitellata Raf. Med. Rep. N. Y. 5:354. 1808, ex char.
Asclepias fragrans Raf. loc. cit. 1808, ex char.
Asclepias pubigera Dum. Fl. Belg. 52. 1827, ex char.
Asclepias elliptica Raf. Aut. Bot. 179. 1840, ex char.
Asclepias serica Raf. loc. cit. 1840, ex char.
Asclepias cornuti Dcne. in DC. Prodr. 8:564. 1844. [Based on *A. syriaca* L.]
Asclepias grandifolia Bert. in Mem. Accad. Sci. Bologna 3:189. 1851, ex char.
Asclepias kansana Vail, in Bull. Torrey Bot. Club 31:457, *pl. 16, fig. 44; pl. 18.* 1904. [T.: *Norton 763*, NY!]
Asclepias intermedia Vail, loc. cit. 459, *pl. 16, fig. 2; pl. 17, figs. 2 a-f.* 1904. [T. *Bicknell s. n.*, NY!]
Asclepias syriaca f. *inermis* Churchill, in Rhodora 20:207. 1919. [T.: *Churchill s. n.*, MO!]
Asclepias syriaca var. *kansana* (Vail) Palmer & Steyerm. in Ann. Missouri Bot. Gard. 22:621. 1935.
Asclepias syriaca f. *leucantha* Dore, in Rhodora 46:387. 1944, ex char. [T.: *Dore s. n.*]

Herbaceous perennials from rather deep gemmiferous roots. Stems stout, usually simple, 1–2 m. tall, finely tomentulose above, becoming glabrate. Leaves opposite, petiolate, broadly ovate or oval to rather narrowly oblong-elliptic, apex acute to rounded, base obtuse to rounded, 6–30 cm. long, 3–10 cm. broad, firmly membranaceous, persistently tomentulose beneath, glabrate above; petioles about 1 cm. long. Inflorescences solitary and lateral at few or several upper nodes, usually many-flowered; peduncles stout, 2–12 cm. long, finely tomentulose; pedicels relatively slender, 2–5 cm. long, finely tomentulose. Flowers moderately large; calyx lobes ovate-lanceolate, 3–4 mm. long, minutely puberulent or tomentulose; corolla reflexed-rotate, usually rose or purplish, rarely white, the lobes 7–9 mm. long; gynostegium shortly stipitate, pale rose, rarely white, the column broadly obconic, 1.0–1.5 mm. long, 2–3 mm. broad, the hoods cucullate, ovate, spreading, 4–5 mm. long, the horn basally adnate, falciform and incurved, somewhat shorter than the hood, the anther head truncately conic, about 2 mm. long and 3 mm. broad. Follicles erect on deflexed pedicels, broadly or narrowly fusiform, usually rather shortly apiculate, very variable, 7–12 cm. long, 2–4 cm. thick, smooth or softly spinose, more or less densely tomentulose; seeds oval, 6–8 mm. long, the white coma 3–4 cm. long.

Prairies and alluvial bottoms, spreading to meadows, fields, roadsides, and railways. Maine to Virginia and westward to North Dakota and Kansas, introduced locally in Georgia, Oklahoma, and Oregon; southern Canada from New Brunswick to Manitoba. Blooming from June to August.

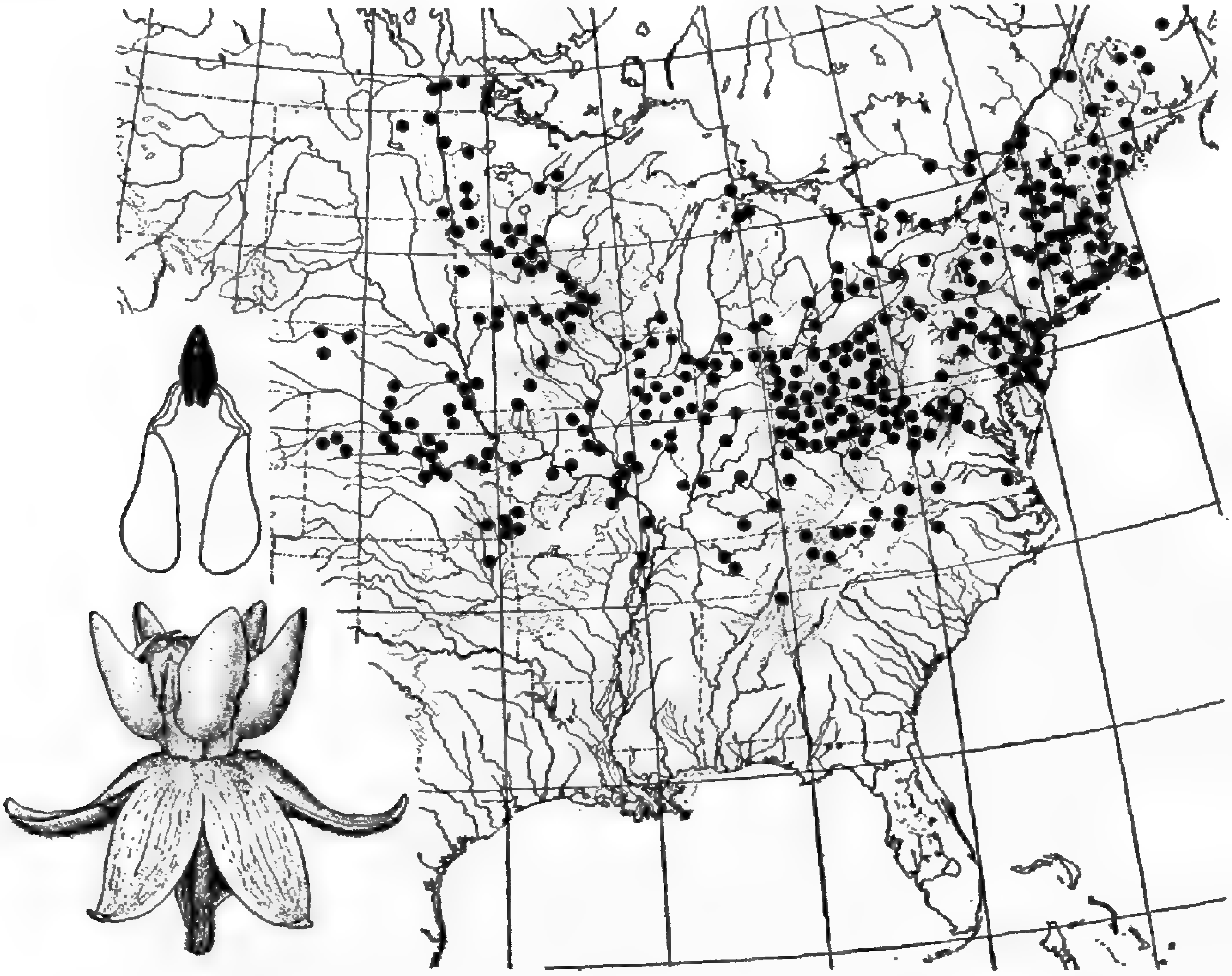

Fig. 42. *Asclepias syriaca* L.

CANADA: MANITOBA: Elmwood, St. Boniface, and Winnipeg counties. NEW BRUNSWICK: Carleton and Victoria counties. ONTARIO: Bruce, Carleton, Elgin, Hastings, Huron, Lambton, Lanark, Middlesex, Muskoka, Oxford, Renfrew, Simcoe, and Welland counties. QUEBEC: Beauharnois, Bonaventure, Chambly, Hochelaga, Hull, Montmagny, Montmorency, and Richelieu counties.

UNITED STATES:

CONNECTICUT: Fairfield, Hartford, New Haven, and New London counties.

DELAWARE: New Castle County.

GEORGIA: Charlton and Dade counties.

ILLINOIS: Champaign, Christian, Cook, Fayette, Ford, Jo Daviess, Kankakee, Lake, McHenry, McLean, Macon, Mason, Madison, Ogle, Peoria, Richland, St. Clair, Sangamon, Stark, Tazewell, Union, Vermilion, and Woodford counties.

INDIANA: Gibson, Harrison, Jasper, Kosciusko, Lake, Marion, Marshall, Monroe, Porter, Steuben, Tippecanoe, and Vermillion counties.

IOWA: Allamakee, Black Hawk, Chickasaw, Clay, Emmet, Fayette, Floyd, Kossuth, Lee, Madison, Mitchell, Palo Alto, Pottawatamie, Story, and Winneshiek counties.

KANSAS: Cherokee, Clay, Cloud, Crawford, Decatur, Dickinson, Geary, Jefferson, Osborne, Republic, Riley, Saline, Shawnee, Sheridan, Sherman, Smith, Thomas, and Wabaunsee counties.

KENTUCKY: Fayette, Pendleton, Taylor, and Warren counties.

MAINE: Androscoggin, Aroostook, Cumberland, Franklin, Kennebec, Oxford, Penobscott, Piscataquis, Sagadahoc, Somerset, and York counties.

MASSACHUSETTS: Barnstable, Berkshire, Bristol, Dukes, Essex, Franklin, Middlesex, Norfolk, Plymouth, Sussex, and Worcester counties.

MICHIGAN: Calhoun, Cheboygan, Emmet, Ingham, Mackinac, Macomb, and Van Buren counties.

MINNESOTA: Aitken, Anoka, Becker, Benton, Big Stone, Carver, Clearwater, Douglas, Hennepin, Houston, Hutchison, Kandiyohi, Lake of the Woods, Lincoln, Meeker, Otter Tail, Polk, Richland, St. Louis, Scott, Stearns, Wabasha, Winona, and Wright counties.

MISSOURI: Boone, Cape Girardeau, Cooper, Dunklin, Franklin, Jackson, Jasper, Jefferson, Knox, Marion, Pike, Ralls, St. Francois, St. Louis, and Vernon counties.

MONTANA: Hill County.

NEBRASKA: Brown, Cedar, Dodge, Douglas, Franklin, Gage, Hall, Howard, Kearney, Lancaster, Nuckolls, Sarpy, and Thomas counties.

NEW HAMPSHIRE: Belknap, Cheshire, Coos, Grafton, Hillsborough, Merrimack, and Rockingham counties.

NEW JERSEY: Burlington, Camden, Cape May, Cumberland, Essex, Mercer, Middlesex, Morris, Salem, and Somerset counties.

NEW YORK: Albany, Cattaraugus, Cayuga, Columbia, Essex, Lewis, Madison, Monroe, Oneida, Oswega, Queens, Rensselaer, St. Lawrence, Schenectady, Steuben, Suffolk, Tioga, Tompkins, Ulster, Warren, and Washington counties.

NORTH CAROLINA: Durham and Surry counties.

NORTH DAKOTA: Benson, Pembina, and Richland counties.

OHIO: Adams, Ashtabula, Athens, Auglaize, Belmont, Brown, Butler, Carroll, Clark, Columbiana, Cuyahoga, Darke, Defiance, Erie, Fairfield, Fayette, Franklin, Fulton, Gallia, Geauga, Greene, Hamilton, Hancock, Harrison, Highland, Hocking, Jefferson, Knox, Licking, Lorain, Madison, Medina, Mercer, Meigs, Miami, Monroe, Montgomery, Noble, Portage, Pickaway, Preble, Richland, Ross, Scioto, Shelby, Summit, Van Wert, Warren, and Wayne counties.

OKLAHOMA: Tulsa County.

OREGON: Marion County.

PENNSYLVANIA: Bedford, Bucks, Carbon, Centre, Chester, Delaware, Erie, Juniata, Lancaster, Lebanon, Luzerne, McKean, Monroe, Montgomery, Northampton, Philadelphia, Schuylkill, Snyder, Sullivan, and Union counties.

RHODE ISLAND: Bristol, Newport, Providence, and Washington counties.

SOUTH DAKOTA: Clay County.

TENNESSEE: Campbell, Carter, Davidson, Hawkins, Knox, Rutherford, Sevier, and Sullivan counties.

VERMONT: Addison, Bennington, Caledonia, Chittenden, Orange, Orleans, Rutland, and Windham counties.

VIRGINIA: Bedford, Fauquier, Frederick, Giles, Isle of Wight, Patrick, and Smyth counties.

WEST VIRGINIA: Barbour, Braxton, Calhoun, Hampshire, Hardy, Harrison, Jackson, Marshall, Mineral, Monongalia, Ohio, Pendleton, Pocahontas, Putnam, Randolph, Ritchie, Upshur, Wetzel, and Wirt counties.

WISCONSIN: Jefferson and Vernon counties.

Asclepias syriaca is the preeminent weedy species of the northeastern United States and this compilation of its distribution is far from complete. It apparently hybridizes occasionally with *A. amplexicaulis,* and such a putative hybrid is *A. intermedia* Vail; in its western range, however, hybridization with *A. speciosa* is rather more frequent, and has been performed experimentally by Prof. O. A Stevens of the North Dakota Experiment Station.

The most variable structure of *A. syriaca* seems to be the fruit, different clones or colonies frequently developing a more or less consistent form of shape and size.[1] A more significant phenomenon is a wide east-west cline with regard to the surface: the western plants being the most spiny and the eastern least so and frequently quite smooth. Doubly interesting is the complementary cline of fruits of *A. speciosa,* which range from spiny in the east to smooth in the west. The two species, although placed in different series here, are in fact extremely difficult to distinguish in the Midwest when not in flower.

37. Asclepias humistrata Walt. Fl. Carol. 105. 1788, ex char.

Asclepias amplexicaulis Michx. Fl. Bor.-Amer. 1:115. 1803, non Sm., ex char.

Prostrate or decumbent herbaceous perennials from a deep narrowly fusiform rootstalk. Stems rather stout, simple, 2–4 dm. long, glaucous, glabrous. Leaves opposite, sessile, very broadly ovate, apex broadly acute to obtuse, base deeply cordate and amplexicaul, 5–12 cm. long, 3–10 cm. broad, glabrous, somewhat subsucculent, glaucous, the veins usually reddish or purplish. Inflorescences terminal and usually lateral from few of the uppermost nodes, several- to many-flowered;

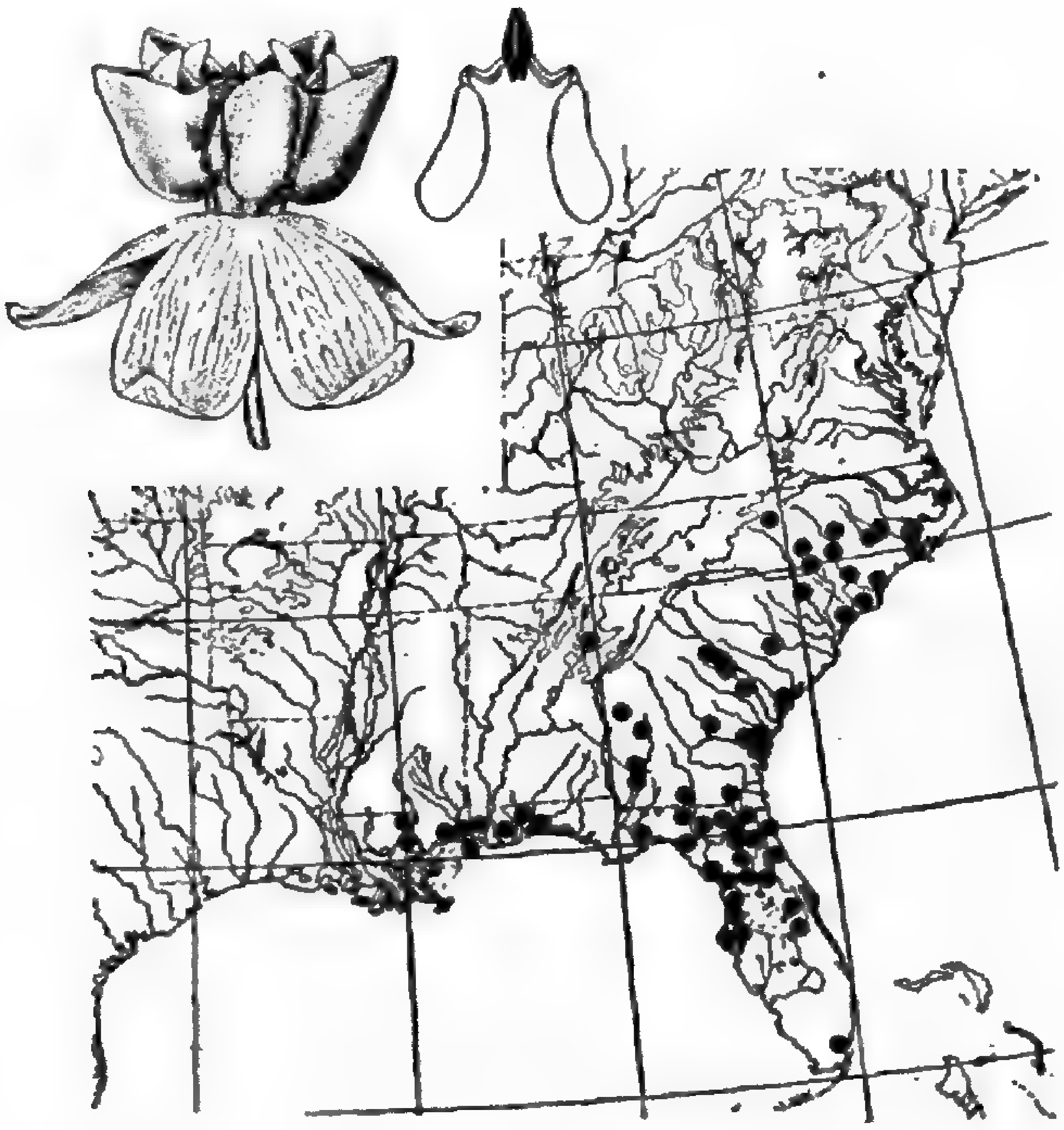

Fig. 43. *Asclepias humistrata* Walt.

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[1] My friend Dr. F. K. Sparrow (Jour. Agr. Res. 73:65. 1946) has described and figured 49 distinct pod types from twelve counties of the Lower Peninsula of Michigan. He cites 38 of these as occurring on a single experimental plot of one acre, thus indicating the variation to be genetic. Since Michigan is about midway of the cline between the predominantly spiny-fruited western races and the predominantly smooth-fruited eastern races of *A. syriaca,* the striking variation in that area may be due to recombination rather than to particularly epidemic mutation affecting the fruit.

peduncles 4–6 cm. long, somewhat slender; pedicels slender, 1–3 cm. long. Flowers rather small; calyx lobes lanceolate, 2.5–3.0 mm. long; corolla reflexed-rotate, purplish rose, the lobes 5–6 mm. long; gynostegium pale purplish cream, shortly stipitate, the column broadly obconic, about 1 mm. long and 1.5–2.0 mm. broad, the hoods cucullate, very broadly ovate, about 3 mm. long, the horn basally adnate, falciform and incurved, slightly shorter than the hood, the anther head truncately conic, 1.5–2.0 mm. long. Follicles erect on deflexed pedicels, narrowly fusiform, 9–10 cm. long, 1.5–2.0 cm. thick, smooth, glabrous; seeds broadly oval, about 8 mm. long, the white coma 3.1–3.5 cm. long.

Sand dunes, dry oak woods, and pine barrens. North Carolina to Florida and westward to Louisiana. Blooming from April to July.

UNITED STATES:

ALABAMA: Baldwin and Mobile counties.

FLORIDA: Alachua, Baker, Bradford, Citrus, Clay, Columbia, Dade, Duval, Escambia, Hernando, Hillsborough, Lafayette, Lake, Levy, Madison, Marion, Orange, Osceola, Pasco, Pinellas, Putnam, St. Johns, Santa Rosa, Sumter, Suwannee, Volusia, and Wakulla counties.

GEORGIA: Baker, Burke, Charlton, Columbia, Dooly, Dougherty, Floyd, Liberty, Long, Lowndes, McIntosh, Richmond, Screven, Taylor, and Wheeler counties.

LOUISIANA: St. Tammany and Washington parishes.

MISSISSIPPI: Harrison and Jackson counties.

NORTH CAROLINA: Bladen, Brunswick, Carteret, Cumberland, Forsyth, Lenoir, Moore, New Hanover, Richmond, and Wayne counties.

SOUTH CAROLINA: Beaufort, Calhoun, Darlington, and Horry counties.

Asclepias humistrata appears to hybridize occasionally with *A. amplexicaulis.*

38. **ASCLEPIAS MEADII** Torr. ex A. Gray, Man. Bot. ed. 2, Add. 704. 1857. [T.: *Mead s. n.,* MO!]

Herbaceous perennials from a slender rootstalk. Stems rather slender, simple, 2–4 dm. tall, glabrous, glaucous. Leaves opposite, sessile, broadly ovate to ovate-lanceolate, apex acute to obtuse, base broadly obtuse to rounded, 5–7 cm. long, 1–5 cm. broad, firmly membranaceous or somewhat subsucculent, glabrous, glaucous. Inflorescences terminal and solitary, few- to several-flowered; peduncles 5–8 cm. long, rather stout; pedicels rather slender, 1.0–1.5 cm. long. Flowers rather large; calyx lobes lance-trigonal, 3–5 mm. long; corolla greenish cream more or less tinged with purple without, the lobes 7–9 mm. long; gynostegium greenish cream, very shortly stipitate, the column very broadly obconic, about 1.5 mm. long and 2.5 mm. broad, the hoods cucullate, very broadly oval, about 5 mm. long, the horn adnate toward the base, incurved and falciform, somewhat shorter than the hood, the anther head truncately conic, about 2 mm. long and 3 mm. broad. Follicles erect on deflexed pedicels, narrowly fusiform, 8–10 cm. long, about 1 cm. broad, glabrous; seeds broadly oval, about 8 mm. long, the white coma about 4 cm. long.

Dry upland prairies and chert-lime glades, very scattered and rare. Southern Wisconsin and northern Illinois westward to Missouri and eastern Kansas. Blooming from May to June.

Fig. 44. *Asclepias meadii* Torr.

United States:
Illinois: Hancock and Peoria counties.
Iowa: Decatur and Scott counties.
Kansas: Allen and Miami counties.
Missouri: Benton, Cass, Iron, Polk, and St. Louis counties.
Wisconsin: Grant County.

An exceedingly elusive little species in spite of the considerable area of its distribution. It has been collected only twice by my friend Dr. J. A. Steyermark, who has long been our most constant and critical student of the Missouri flora. I have never found it, although I have visited promising localities upon a number of occasions.

39. Asclepias hypoleuca (A. Gray) Woodson, in Ann. Missouri Bot. Gard. 28:206. 1941.

Gomphocarpus hypoleucus A. Gray, in Proc. Amer. Acad. 17:222. 1881. [T.: *Pringle s. n.*, MO!]

Herbaceous perennials. Stems rather stout, simple or rarely branching below ground, 1.5–6.0 dm. tall, finely tomentulose above to glabrate below. Leaves opposite, petiolate, broadly oblong-ovate or oval to rather narrowly oblong-elliptic, apex broadly acute to rounded, base broadly rounded, 2.5–12.0 cm. long, 2–5 cm. broad, firmly membranaceous, dark green and glabrate above, paler and densely white-tomentulose beneath; petioles 0.3–1.0 cm. long. Inflorescences usually terminal and solitary, rarely lateral also at the uppermost node, several- to many-flowered; peduncles 2–8 cm. long, rather stout; pedicels rather slender, 1–2 cm. long. Flowers large and showy; calyx lobes ovate-lanceolate, 5–6 mm. long, densely and minutely tomentulose; corolla reflexed-rotate, deep red, the lobes 1.0–1.2 cm. long; gynostegium deep red or purplish, stipitate, the column obconic, about 2 mm. long and 2.0–2.5 mm. broad, the hoods cucullate, lanceolate, narrowly but obtusely acuminate, with very prominent marginal lobes, spreading, 7–9 mm. long, the horn when present very short and stout and very strongly adnate, apparently most frequently absent or reduced to a mere fleshy pad, the anther head truncately conic, about 2.5 mm. long and 3.5 mm. broad. Follicles erect on deflexed pedicels, unknown when mature.

Yellow pine forests in mountains, widespread but infrequent, rarely spreading to open fields. Southern New Mexico and Arizona; northern Chihuahua and northeastern Sonora. Blooming from June to August.

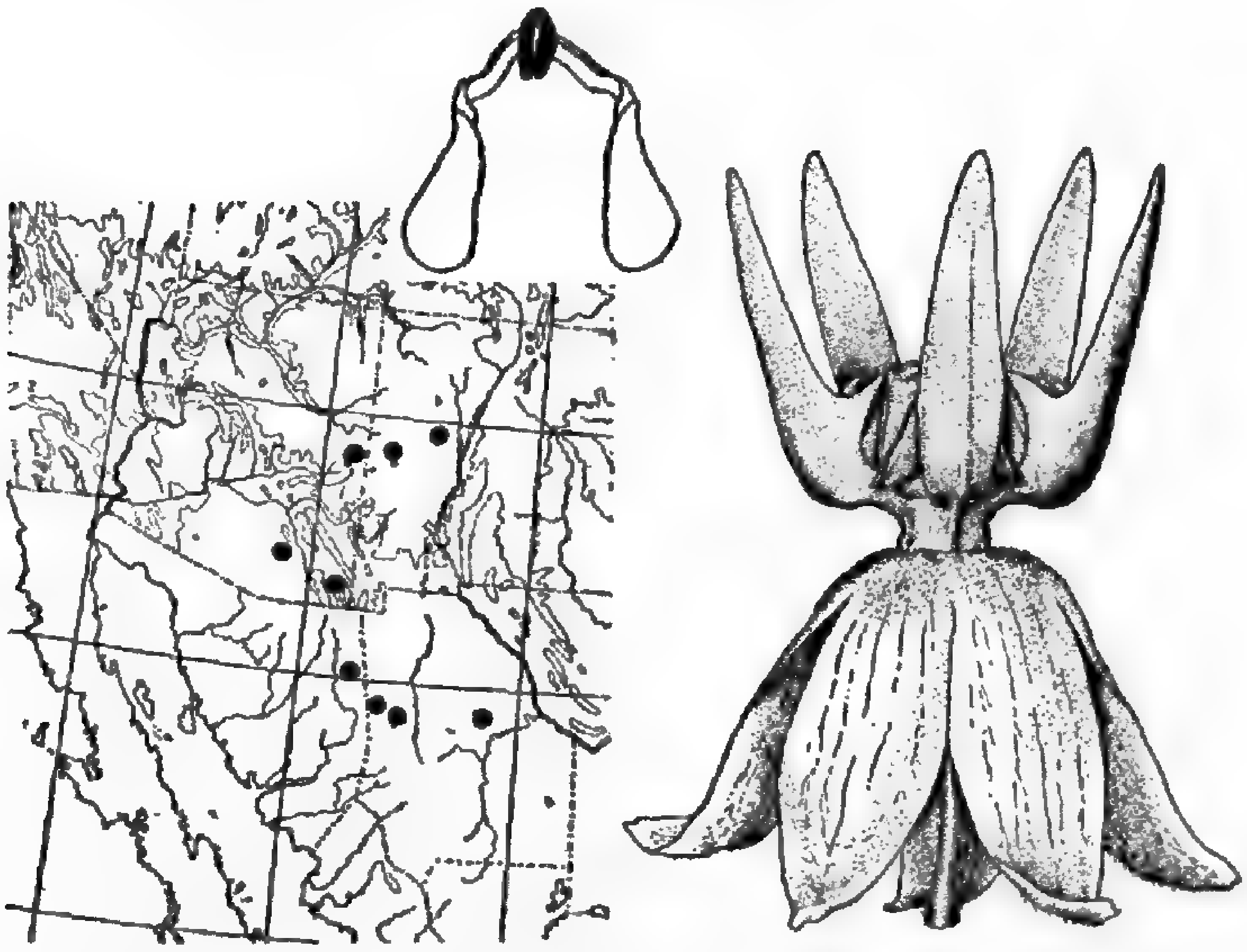

Fig. 45. *Asclepias hypoleuca* (A. Gray) Woods.

UNITED STATES:
ARIZONA: Apache, Cochise, and Pima counties.
NEW MEXICO: Catron and Socorro counties.
MEXICO: CHIHUAHUA: Concheño, Colonia García, Pinos Altos. SONORA: Puerto de los Aserraderos.

As rather frequently seems to be the case, the most obvious relationship of this handsome species appears to be *A. laxiflora* of series MACROTIDES, which has a very similar general aspect. *A. hypoleuca* is placed in SYRIACAE because of the very prominent marginal lobes of the hoods.

40. ASCLEPIAS PRINGLEI (Greenm.) Woodson, in Ann. Missouri Bot. Gard. 28:206. 1941.

Acerates humilis Benth. Pl. Hartw. 291. 1848, non *Asclepias humilis* Schltr. [T.: *Hartweg s. n.*, K!]
Acerates Pringlei Greenm. in Proc. Amer. Acad. 34:570. 1899. [T.: *Pringle 6853*, MO!]
Asclepias constricta M. E. Jones, Contr. West. Bot. 12:49. 1908. [T.: *Jones 318*, MO!]
Asclepias phenax Woodson, in Ann. Missouri Bot. Gard. 28:206. 1941. [Based on *Acerates humilis* Benth.]

Herbaceous perennials from short fleshy horizontal rhizomes, the roots unusually thick and fleshy. Stems rather stout, simple, thickly clustered from the rhizome, 1–5 dm. tall, densely and minutely puberulent when young, becoming glabrate. Leaves opposite, shortly petiolate, very broadly ovate to oblong-elliptic, apex broadly obtuse to acuminate, base obtuse to rounded or very broadly cordate, 4–15 cm. long, 2–7 cm. broad, firmly membranaceous, dark green above, glaucous beneath, generally puberulent, particularly beneath; petioles 0.7–1.3 cm. long. Inflorescences solitary and lateral at few to several upper nodes, usually many-flowered; peduncles rather stout, 2.5–10.0 cm. long, densely and minutely puberulent; pedicels rather slender, 1–2 cm. long. Flowers rather small; calyx lobes lanceolate, about 3 mm. long; corolla white usually tinged with purple without, the lobes 5–7 mm. long; gynostegium shortly stipitate, white, the column very broadly obconic, 0.5–1.0 mm. long and about 2 mm. broad, the hoods cucullate, oblong-ovate, somewhat spreading, about 3 mm. long, the horn frequently absent but when present strongly adnate, subacicular, much shorter than the hood, the anther head truncately conic, about 1.5 mm. long and 2.5–3.0 mm. broad. Follicles on pendulous peduncles, ovoid to broadly fusiform, 5–7 cm. long, 3–4 cm. broad, smooth, minutely pilosulose to glabrate; seeds broadly oval, about 9 mm. long, naked.

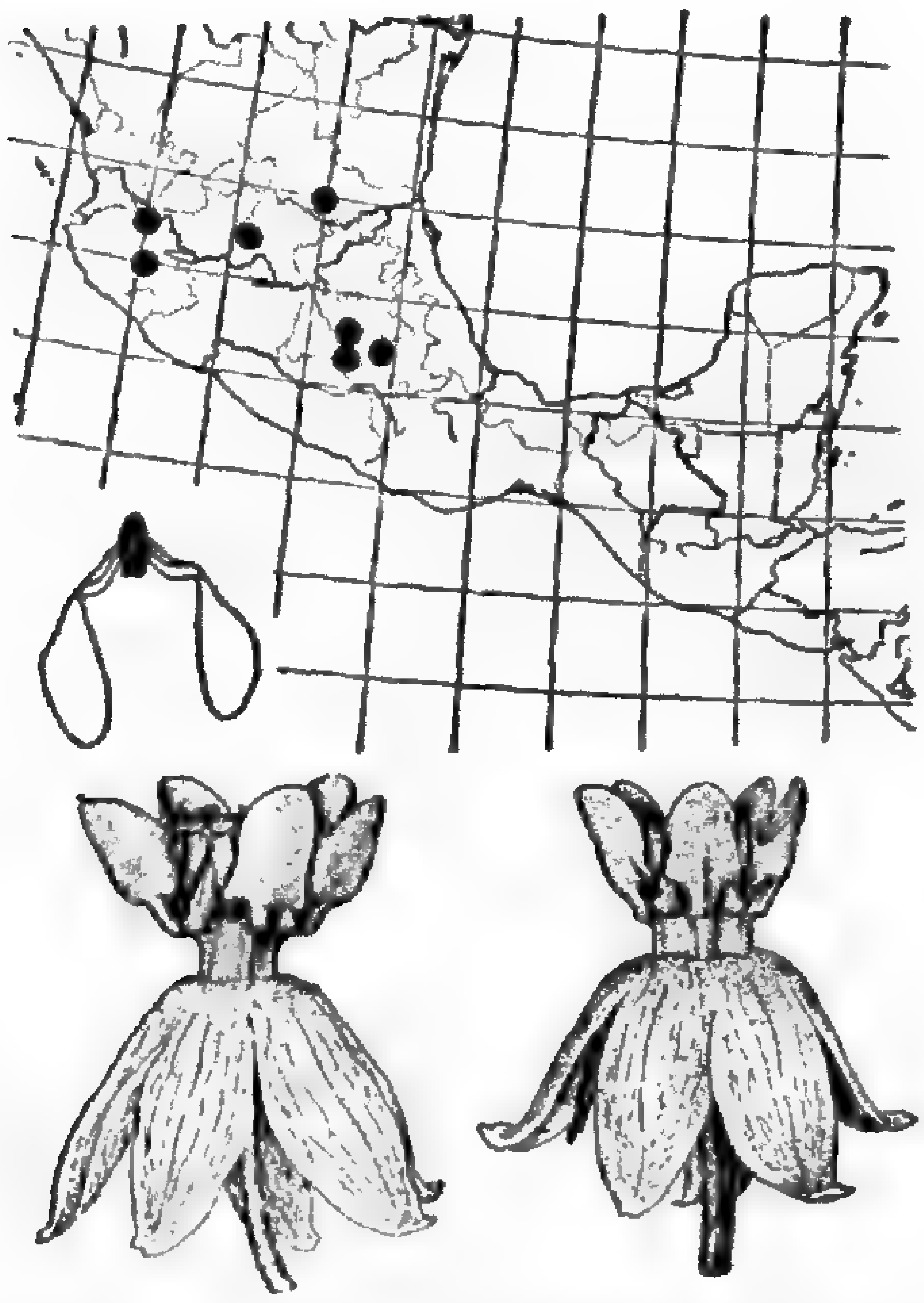

Fig. 46. *Asclepias pringlei* (Greenm.) Woods.

Open places in fir or pine woods, rocky meadows. South-central Mexico. Blooming from May to July.

MEXICO: GUANAJUATO: León. JALISCO: Tapalpa, Nevada de Colima, Mesquites, Monte Escobrado. MEXICO: El Judío, Monte de Río Frío, Plan de Salazar, Camino de Toluca, Temascaltepec. MORELOS: Serranía de Ajusco, El Parque. PUEBLA: Ixtaccihuatl. SAN LUIS POTOSÍ: Alvarez.

Like those of *A. pellucida*, the naked seeds of *A. pringlei* would appear to be modified for dissemination by water, but such does not seem to be the case! *Asclepias pringlei* is suspected of occasional hybridization with *A. lanuginosa*, and the evidence will be discussed under the latter species.

The frequent absence of a corona horn led both Bentham and Greenman to assign this species to *Acerates*. I believe that the horned condition may be even more frequent, however, and in all other respects *A. pringlei* has nothing in common with subgen. ACERATES.

41. ASCLEPIAS PRATENSIS Benth. Pl. Hartw. 45. 1840. [T.: *Hartweg 345*, K!]

Herbaceous perennials. Stems rather slender, in small clusters from the rhizome, simple or with few weak branches from the base, 2–4 dm. tall, glabrous, glaucous. Leaves opposite, sessile or subsessile, ovate to lanceolate, apex acute to obtuse, base broadly obtuse or rounded, 4–8 cm. long, 1.5–3.0 cm. broad, firmly membrana-

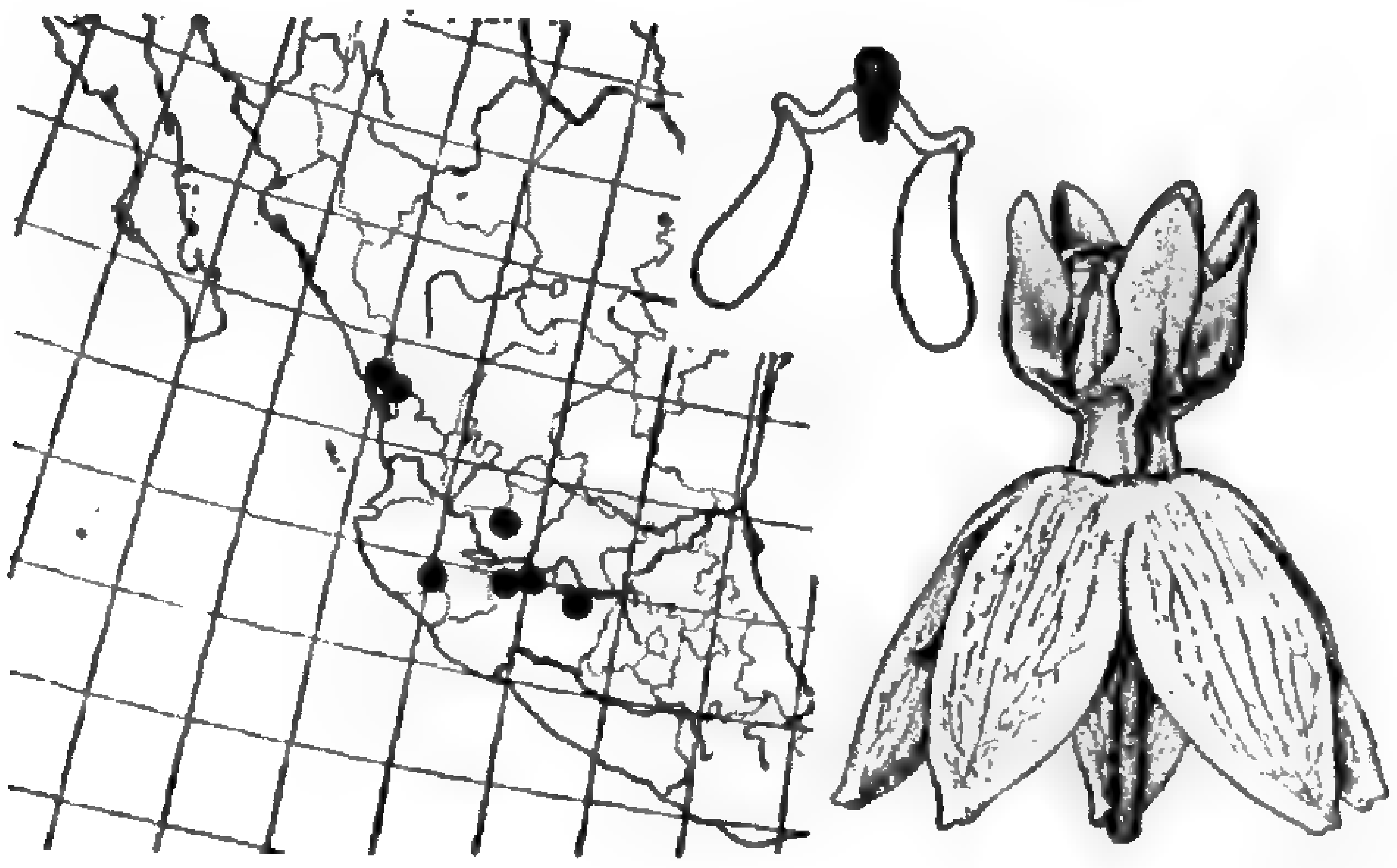

Fig. 47. *Asclepias pratensis* Benth.

ceous, glabrous, glaucous. Inflorescences solitary and terminal or lateral from few of the upper nodes, few- to several-flowered; peduncles rather slender, 1–3 cm. long; pedicels slender, 1.5–2.5 cm. long. Flowers rather small; calyx lobes ovate-lanceolate, about 3 mm. long; corolla reflexed-rotate, pale greenish white sometimes tinged with purple without, the lobes 5–7 mm. long; gynostegium shortly stipitate, white or cream, the column obconic, about 1.5 mm. long and broad, the hoods cucullate, broadly ovate, 3.5–4.0 mm. long, the horn about half adnate, falciform, somewhat shorter than the hood, the anther head truncately conic, 2.0–2.5 mm. long and 2.5–3.0 mm. broad. Follicles erect on deflexed pedicels, rather narrowly fusiform, 7–10 cm. long, about 1.5 cm. broad; seeds unknown.

Wet or low meadows, spreading to fields. South-central Mexico. Blooming from June to July.

MEXICO: JALISCO: Guadalajara, Hacienda San Marcos. MICHOACAN: Loma Santa María, Morelia, Punguato, Lake Pátzcuaro. SINALOA: Rosario, Acaponeta.

A very homogeneous little species, superficially resembling *A. ovalifolia.*

42. ASCLEPIAS LINARIA Cav. Ic. 1:42, *t. 57.* 1791. [T.: Herb. Cav., MO, photo!]

Asclepias filiformis Sessé & Moc. Pl. Nov. Hisp. 43. 1887. [T.: *Sessé & Moc. s. n.*, F!]
Asclepias pinifolia Greene, in Bull. Torrey Bot. Club 8:5. 1881, ex char. [T.: *Greene s. n.*]

Rather low, twiggy shrubs or suffruticose herbs 0.5–2.0 m. tall. Stems relatively slender, more or less woody and bearing the persistent bases of past leaves, branching repeatedly, minutely pilosulose when young, soon becoming glabrate. Leaves spirally approximate, crowded, sessile, filiform or acicular, 2–5 cm. long, about 1 mm. broad, revolute, rather rigid, scatteringly pilosulose to glabrate. Inflorescences lateral and solitary at few or several of the upper nodes, several- to many-flowered; peduncles moderately slender, 0.5–2.0 cm. long, pilosulose; pedicels slender, 1.5–2.0 cm. long, pilosulose. Flowers rather small, rotate or reflexed-rotate; calyx lobes lanceolate, about 3 mm. long, minutely pilosulose; corolla greenish white usually flushed with rose or purple without, the lobes 4–5 mm. long; gynostegium shortly stipitate, cream or orange (?), the column obconic, about 1 mm. long and broad, the hoods cucullate, broadly ovate, 3–4 mm. long, the horn almost wholly adnate, much shorter than the hoods, the anther head truncately conic, about 1.5 mm. long and 2.5–3.0 mm. broad. Follicles erect on deflexed pedicels, rather broadly fusiform or napiform, narrowly attenuate, 4–5 cm. long, 1–2 cm. broad, smooth, scatteringly pilosulose to glabrate; seeds oval, about 6 mm. long, the white coma about 2 cm. long.

Open oak, pine, and juniper woodlands, dry limestone ridges, rocky hills, sandy volcanic slopes, canyons and arroyos, spreading to dry pastures and wasteland. Southern Arizona and adjacent California; virtually throughout highland Mexico. Blooming from April to November.

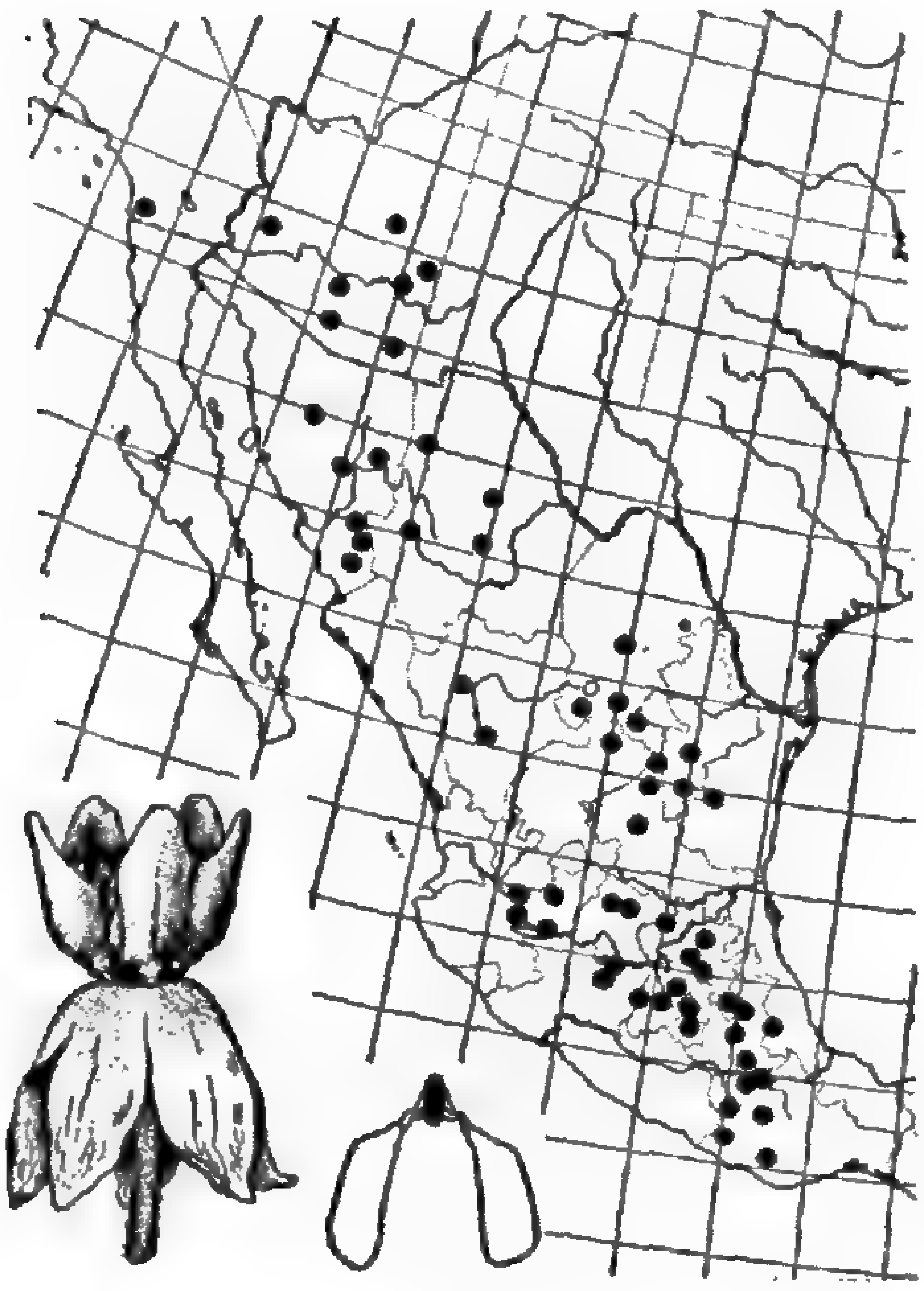

Fig. 48. *Asclepias linaria* Cav.

UNITED STATES:

ARIZONA: Cochise, Gila, Graham, Greenlee, Pinal, Pima, and Yuma counties.

CALIFORNIA: San Diego County.

MEXICO: CHIHUAHUA: Sierra Charuco, Sierra Azul, Mapula, Chihuahua, Pinos Altos. COAHUILA: Saltillo, G. Cepeda, Arteaga, Fraile, Mt. Jimulco. DISTRITO FEDERAL: Contreras, Tlalpam, San Angel, Tizapan, Valle de Mexico, Lomas de Santa Fé, El Peñon, Olivar. DURANGO: Durango, San Ramón, Tobar. GUANAJUATO: Empalme de Gonzales, Guanajuato, Silao. HIDALGO: Ixmiquilpan, Jacala, Pachuca, Zimapán, Tasquillo. JALISCO: Lake Chapala, Tuxcueca, San Luis Capistrano, Huejuquilla, Villa Guadalupe, Real Alto. MEXICO: Toluca, Temascaltepec. MICHOACAN: Morelia, Santa Fé, Quirogo, Zitacuaro, Mt. Patamban. MORELOS: Tepoztlán. NUEVO LEÓN: Galeana, Doctor Arroyo. OAXACA: Mitla, Ocotlán, Coixtlahuaca, Tamazulapam, Misteca, Tlaxiaco, Teposcolula. PUEBLA: Puebla, Noria, Tehuacán, Cerro de Guadalupe, Atlixco. QUERETARO: Quarétaro, Hacienda Ciervo. SAN LUIS POTOSÍ: San Luis Potosí, Charcas. SONORA: Pilares de Nacozari, Sierra del Pajarito, Magdalena, Los Pinitos, Aribabi, Puerto de Huépari, Río Mayo, Sierra Charuco, Río de Bavispe. TAMAULIPAS: Miquihuana. TLAXCALA: Tetlanochan. VERACRUZ: Orizaba, Acultzinco. ZACATECAS: Real de Pinos, Cedros, Concepción del Oro, Villa Nueva.

Asclepias linaria is such a characteristic and uniform species throughout its rather vast range that it is disappointing to find only two popular names recorded for it: the usual *lechetresna* in the State of Mexico, and *yerba de cuervo* in Sonora. This is one of the woodiest of the American species of *Asclepias,* and the branches and leaves might almost be mistaken for pine seedlings, as many collectors have noted.

Series 6. PURPURASCENTES

KEY TO THE SPECIES

a. Plants erect (decumbent in *A. curtissii*), relatively stout.
  b. Hoods somewhat less than twice as long as the anther head, very broadly rounded at the tip.

c. Hoods not conduplicate; anther wings very conspicuously spurred at the base; flowers dull purplish rose; leaves sessile or subsessile. Southern Ontario; Ohio westward to eastern Nebraska and Oklahoma ....43. *A. sullivantii*

cc. Hoods conduplicate; anther wings rather inconspicuously notched at the base; flowers white with a purple column; leaves distinctly petiolate. Connecticut to Florida and westward to southern Missouri and eastern Texas ....44. *A. variegata*

bb. Hoods more than twice as long as the anther head, acute to acuminate.

c. Hoods two to three times as long as the anther head, abruptly acute to acuminate, erect or only slightly spreading.

d. Plants erect; flowers purplish rose, moderately large.

e. Plants essentially glabrous; leaves definitely petiolate.

f. Leaves opposite, broadly oval to ovate-oblong, obtuse. Southern Ontario; New Hampshire to Virginia and westward to eastern Kansas........45. *A. purpurascens*

ff. Leaves irregularly approximate, narrowly ovate to lanceolate, acute to obtusely acuminate. Wyoming and Colorado to Utah and Nevada........46. *A. hallii*

ee. Leaves densely white-tomentose beneath, typically very broadly ovate, cordate, sessile and amplexicaul (shortly petiolate or even nearly glabrous in putative hybrids). San Luis Potosí to Oaxaca ....47. *A. lanuginosa*

dd. Plants decumbent; flowers greenish white, rather small. Peninsular Florida........48. *A. curtissii*

cc. Hoods three to four times as long as the anther head, gradually acuminate, widely spreading; plants densely tomentulose generally, particularly the inflorescence. Southern Manitoba to southern British Columbia; western Minnesota to northwestern Texas and westward to the Pacific Coast ....49. *A. speciosa*

aa. Plants prostrate, very small in all parts; flowers pale pink; hoods twice as long as the anther head, broadly rounded at the tip. San Luis Potosí and Durango......50. *A. euphorbiaefolia*

43. **Asclepias sullivantii** Engelm. ex A. Gray, Man. Bot., ed. 1, 366. 1848. [T.: *Sullivant s. n.*, MO!]

Herbaceous perennials from a rather deep, fleshy rootstalk. Stems rather stout, simple, 6–9 dm. tall, glabrous and somewhat glaucous. Leaves opposite, sessile or subsessile, broadly oval or ovate to narrowly oblong or oblong-lanceolate, apex broadly obtuse or rounded, base broadly rounded to broadly and shallowly cordate and somewhat amplexicaul, 9–15 cm. long, 2–9 cm. broad, firmly membranaceous or somewhat succulent, glabrous, slightly glaucous. Inflorescences lateral at few to several upper nodes, several- to many-flowered; peduncles rather stout, 1–6 cm. long, glabrous; pedicels rather more slender, 2–4 cm. long. Flowers rather large; calyx lobes lance-elliptic, 5–6 mm. long; corolla purplish rose, the lobes 9–11 mm. long; gynostegium pale rose, shortly stipitate, the column broadly obconic, about 2 mm. long and 2.5–3.0 mm. broad, the hoods cucullate, broadly oval, 5–6 mm. long, the horns adnate about midway, falciform, abruptly incurved, somewhat shorter than the hood, the anther head truncately conic, about 3 mm. long and 4 mm. broad. Follicles erect on deflexed pedicels, broadly fusiform and shortly apiculate, 8–10 cm. long, usually more or less spiny, rather inconspicuously appressed-pilosulose to glabrous; seeds broadly oval, about 8 mm. long, the white coma about 4.5 cm. long.

Low prairies, alluvial meadows, and bottom-lands, spreading to roadsides. Southern Ontario; Ohio to Minnesota, Nebraska, and Oklahoma. Blooming from June to August.

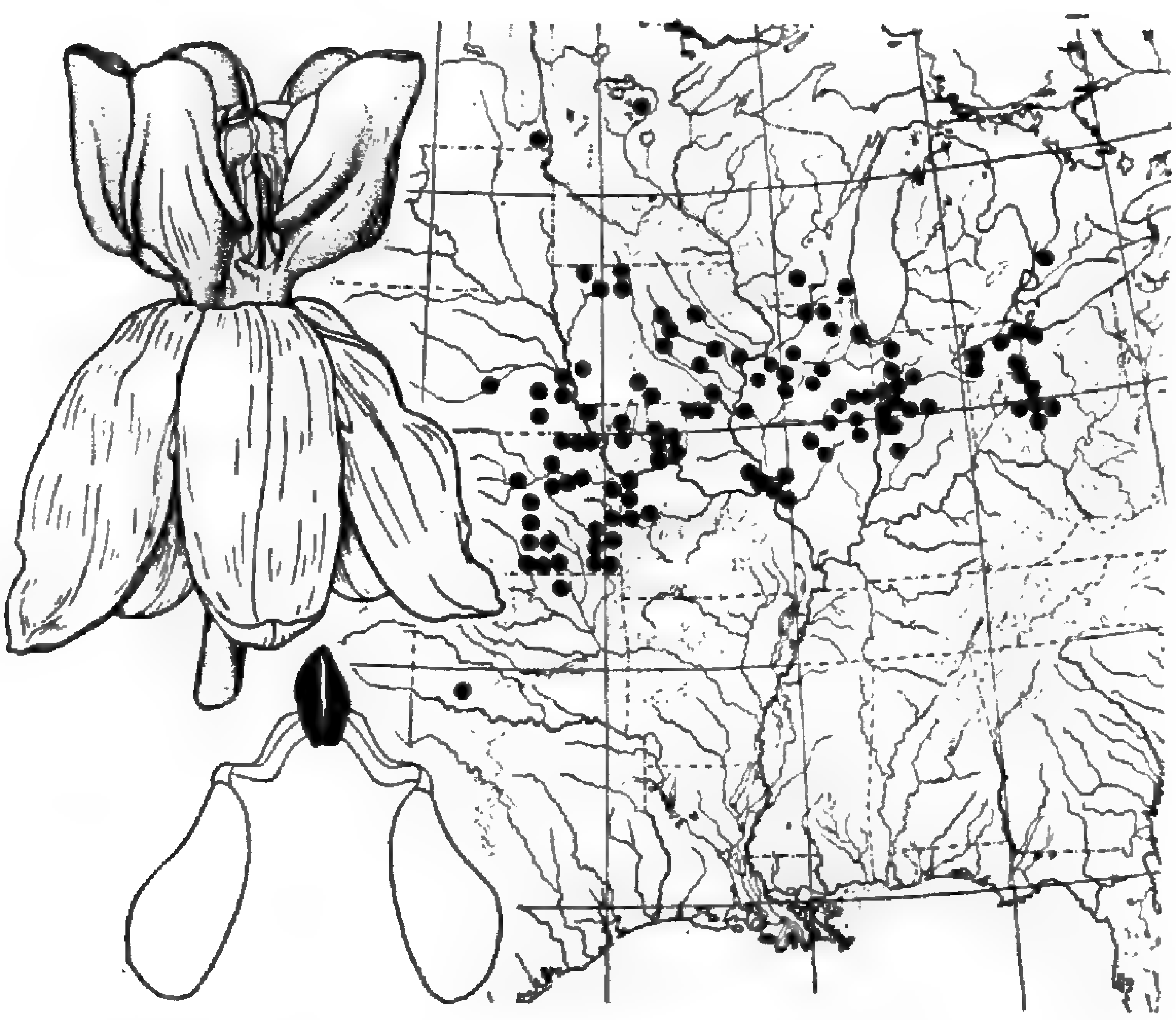

Fig. 49. *Asclepias sullivantii* Engelm.

Canada: ontario: Lambton County.

United States:

illinois: Champaign, Christian, Cook, Douglas, Ford, Fulton, Hancock, Kane, Knox, Livingston, McHenry, McLean, Macon, Madison, Peoria, Piatt, St. Clair, Sangamon, Stark, Vermilion, Will, and Winnebago counties.

indiana: Benton, Cass, Clinton, Jasper, Owen, Parke, Porter, Tipton, Tippecanoe, Vermillion, Warren, and Whites counties.

iowa: Black Hawk, Clay, Decatur, Emmet, Hamilton, Iowa, Mahaska, Muscatine, Osceola, Palo Alto, Polk, Pottawattemie, Story, Union, and Van Buren counties.

kansas: Allen, Bourbon, Brown, Butler, Chautauqua, Cherokee, Cowley, Crawford, Dickinson, Geary, Johnson, Labette, Lincoln, Linn, McPherson, Marshall, Nemaha, Neosho, Ottawa, Riley, Saline, Sedgwick, Shawnee, Sumner, and Wabaunsee counties.

minnesota: Crow Wing County.

missouri: Atchison, Bates, Carroll, Cass, Chariton, De Kalb, Gentry, Grundy, Henry, Jackson, Lincoln, Linn, Livingston, St. Charles, St. Louis, Schuyler, and Scotland counties.

nebraska: Cass, Gage, Hall, Lancaster, Otoe, and Sarpy counties.

north dakota: Richland County.

ohio: Defiance, Delaware, Erie, Fairfield, Franklin, Madison, Marion, Ottawa, Paulding, Pickaway, Wood, and Wyandot counties.

oklahoma: Comanche and Osage counties.

wisconsin: Dane and Racine counties.

One might expect occasional hybrids of *A. sullivantii* and *A. syriaca* or perhaps *A. amplexicaulis*, but I have seen none.

44. Asclepias variegata L. Sp. Pl. 215. 1753. [T.: Linn. Herb. London, no. *310.20*, photo!]

Asclepias citrifolia Jacq. Coll. 2:290. 1788, ex char.
Asclepias hybridus Michx. Fl. Bor.-Amer. 1:115. 1803, ex char.
Asclepias variegata α major Hook. Fl. Bor.-Amer. 2:52. 1838. [*Var. typ.*]
Biventraria variegata (L.) Small, Man. Southeast. Fl. 1072. 1933.

Herbaceous perennials from a fleshy, fusiform rootstalk. Stems rather slender, simple, 3–12 dm. tall, inconspicuously pilosulose in decurrent lines from the nodes. Leaves opposite, petiolate, broadly oval, apex broadly obtuse to broadly acute, base very broadly obtuse or rounded, 8–15 cm. long, 4–9 cm. broad, dark green and glabrous above, glaucous and very sparsely pilosulose beneath; petioles 1–2 cm. long. Inflorescences usually solitary and terminal, occasionally also lateral from very few of the uppermost nodes, rather many-flowered and very compactly hemispherical; peduncles rather slender, 1–7 cm. long; pedicels 1–2 cm. long. Flowers rather large and showy; calyx lobes ovate, about 3 mm. long; corolla rotate, white, the lobes 7–8 mm. long; gynostegium white save the purple column, shortly stipitate, the column obconic, about 1.5 mm. long and 2.0–2.5 mm. broad, the hoods cucullate, conduplicate and inflated, very broadly obovate, about 2.5 mm. long, the horn adnate toward the base, falciform and sharply inflexed, much shorter than the hood, the anther head about 2 mm. long and 3 mm. broad. Follicles erect on deflexed pedicels, narrowly fusiform, gradually apiculate, 10–15 cm. long, 1.5–2.0 cm. thick, glaucous, minutely pilosulose; seeds oval, about 5 mm. long, the white coma 2.5–4.5 cm. long.

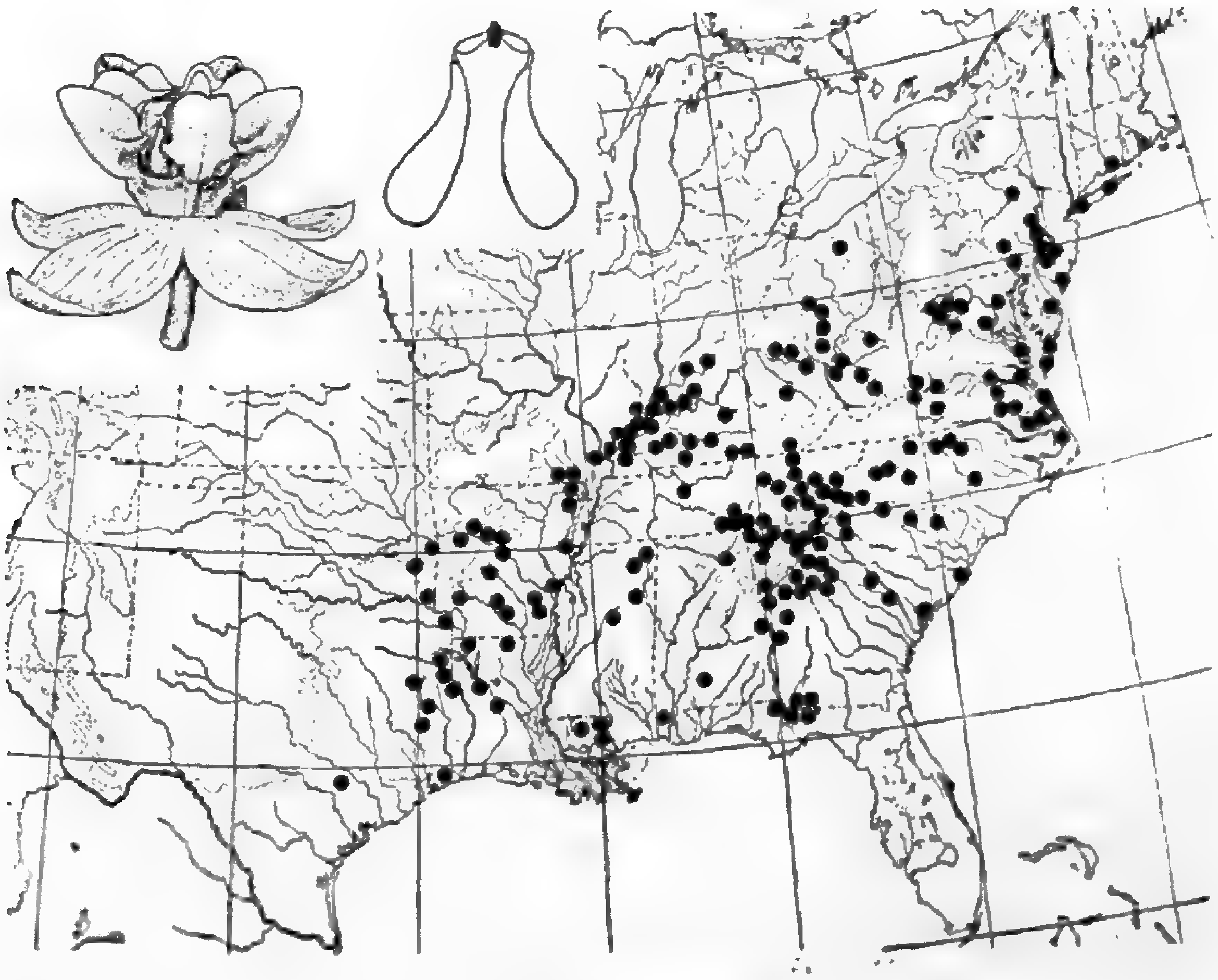

Fig. 50. *Asclepias variegata* L.

Thickets and open woods, usually in sandy or rocky soil. Connecticut to northern Florida and westward to southern Missouri and eastern Texas. Blooming from May to July.

UNITED STATES:

ALABAMA: Conecuh, Lee, Marshall, and Mobile counties.

ARKANSAS: Calhoun, Conway, Craighead, Drew, Faulkner, Greene, Hempstead, Hot Springs, Lincoln, Logan, Ouachita, Phillips, Pope, Pulaski, and St. Francis counties.

CONNECTICUT: Middlesex County.

DELAWARE: Sussex County.

FLORIDA: Gadsden, Jackson, and Leon counties.

GEORGIA: Banks, Barrow, Carroll, Clarke, Cobb, Dade, Dawson, Decatur, De Kalb, Floyd, Forsyth, Fulton, Gwinnett, Heard, Jackson, Meriwether, Murray, Muscogee, Rabun, Richmond, Screven, Thomas, Walker, and White counties.

ILLINOIS: Alexander, Gallatin, Hardin, Johnson, Massac, and Pope counties.

INDIANA: Crawford, Gibson, Jackson, Martin, Perry, Posey, and Spencer counties.

KENTUCKY: Bell, Caldwell, Edmonson, Hopkins, Lewis, Logan, McCracken, McCreary, Nelson, Union, Warren, Whitley, and Wolfe counties.

LOUISIANA: Bossier, Lincoln, Natchitoches, Rapides, St. Tammany, Tangipahoa, and Washington parishes.

MARYLAND: Prince Georges County.

MISSISSIPPI: Attala, Lee, Oktibbeha, and Prentiss counties.

MISSOURI: Butler, Ripley, and Scott counties.

NEW JERSEY: Burlington, Camden, and Cape May counties.

NEW YORK: Queens and Suffolk counties.

NORTH CAROLINA: Alexander, Buncombe, Cumberland, Durham, Forsyth, Haywood, Henderson, Iredell, Macon, Madison, Orange, Pasquotank, Perquimans, Polk, Rowan, Swain, and Wake counties.

OHIO: Adams, Fairfield, Franklin, Hocking, Jackson, Scioto, and Scott counties.

OKLAHOMA: Latimer, Le Flore, and McCurtain counties.

PENNSYLVANIA: Bucks, Lancaster, Lebanon, Luzerne, Northampton, and Philadelphia counties.

SOUTH CAROLINA: Anderson, Beaufort, Charleston, Cherokee, Darlington, Lancaster, and Pickens counties.

TENNESSEE: Blount, Bradley, Davidson, Franklin, Grundy, Hamilton, Knox, Marion, Monroe, Morgan, Roane, Sevier, and Union counties.

TEXAS: Angelina, Bowie, Cherokee, Gonzales, Harrison, Jefferson, Panola, Polk, and Shelby counties.

VIRGINIA: Accomac, Allegheny, Bedford, Campbell, Craig, Dinwiddie, Frederick, Greensville, Henrico, James City, Lancaster, Northampton, Prince George, Prince William, Princess Anne, Shenandoah, and Southampton counties.

WEST VIRGINIA: Cabell, Calhoun, Hampshire, Hardy, Kanawha, Mineral, Raleigh, and Wayne counties.

The glistening white flowers are so tightly compacted into the hemispheric inflorescences that no spaces appear between them, and the general effect is of a small snowball, with an irridescent quality imparted by the purple columns. One of the most beautiful of all milkweeds.

There are no specimens of *A. variegata* labelled as such by Linnaeus or his son in the Linnean Herbarium. However, there are two sheets labelled *A. nivea* obviously in error, and a third labelled *Asclepias dilatata,* a manuscript name perhaps exchanged by Linnaeus for the somewhat more descriptive *variegata.* I am choosing the latter as the lectotype.

45. ASCLEPIAS PURPURASCENS L. Sp. Pl. 214. 1753, ex char.

Asclepias amoena L. loc. cit. 1753, ex char.
Asclepias compressa Moench, Meth. 717. 1794, ex char.
Asclepias dasypus Raf. Atl. Jour. 152. 1832, ex char.
Asclepias lasiotis Raf. Aut. Bot. 178. 1840, ex char.
Asclepias gonialis Raf. loc. cit. 1840, ex char.

Herbaceous perennials. Stems rather stout, simple, 4–10 dm. tall, minutely pilosulose when young, becoming glabrate. Leaves opposite, petiolate, broadly ovate or oval to ovate- or oblong-lanceolate, apex obtuse to acute, base obtuse to broadly rounded and very shortly and abruptly cuneate into the petiole, 6–18 cm. long, 3–10 cm. broad, firmly membranaceous, dark green and glabrate above, paler and densely and generally puberulent below; petioles 0.5–2.5 cm. long. Inflorescences terminal and solitary or paired, occasionally accompanied by very few at the uppermost nodes, several- to rather many-flowered; peduncles rather slender, 1.5–9.0 cm. long, minutely puberulent; pedicels slender, 2.0–3.5 cm. long, minutely puberulent. Flowers rather large and very showy; calyx lobes ovate-lanceolate, 3–4 mm. long, minutely puberulent; corolla deep rose, reflexed-rotate, the lobes 7–10 mm. long; gynostegium deep rose, very shortly stipitate, the column obconic, 1.5–2.0 mm. long, 2.5–3.0 mm. broad, the hoods oblong-elliptic, acute to acuminate, 6–7 mm. long, the horn about half adnate, falciform and sharply incurved, much shorter than the hoods, the anther head truncately conic, about 2 mm. long and 3 mm. broad. Follicles erect on deflexed pedicels, narrowly fusiform, gradually attenuate, 10–16 cm. long, about 1–2 cm. thick, smooth, minutely puberulent to glabrate; seeds oval, 5–6 mm. long, the white coma 3.5–4.5 cm. long.

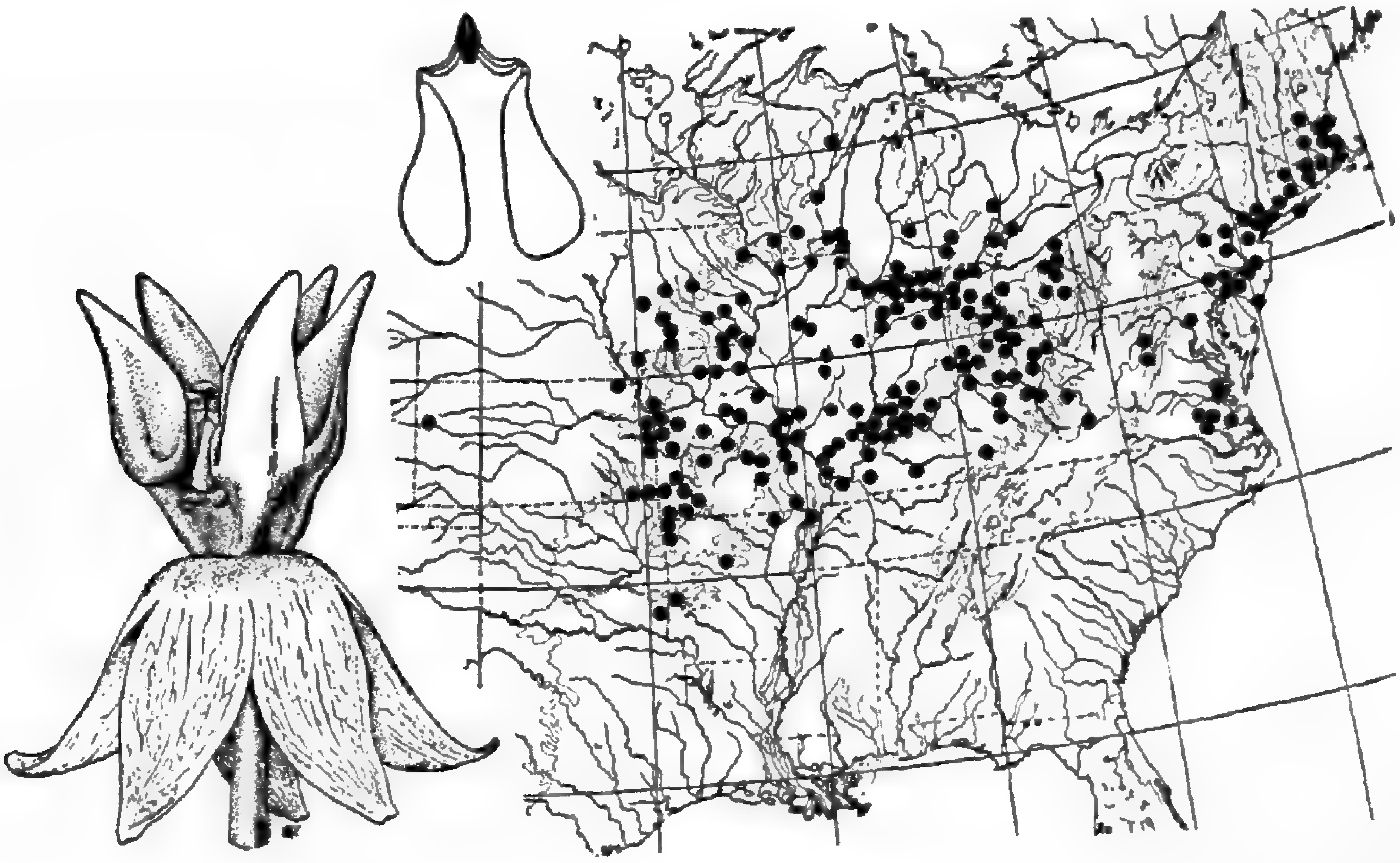

Fig. 51. *Asclepias purpurascens* L.

Thickets and open woods, prairies and fields, spreading to roadsides and railways. Southern Ontario; New Hampshire to Virginia and westward to eastern Kansas.

CANADA: ONTARIO: Essex and Lambton counties.
UNITED STATES:
ARKANSAS: Benton, Faulkner, Polk, Randolph, and Washington counties.
CONNECTICUT: Fairfield, Hartford, New Haven, New London, and Windham counties.
DELAWARE: New Castle County.

DISTRICT OF COLUMBIA.

ILLINOIS: Christian, Cook, Fayette, Jefferson, Jo Daviess, Lake, McHenry, Macon, Madison, Peoria, Pulaski, Randolph, Richland, St. Clair, Union, Vermilion, Wabash, and Wayne counties.

INDIANA: Allen, Cass, Clark, Crawford, Daviess, Dubois, Elkhart, Franklin, Fulton, Gibson, Grant, Greene, Harrison, Knox, Kosciusko, Lake, La Porte, Lawrence, Martin, Noble, Perry, Porter, Pulaski, Spencer, Steuben, Vanderburgh, Warrick, Wells, and White counties.

IOWA: Audubon, Boone, Clarke, Clayton, Decatur, Henry, Iowa, Johnson, Lee, Madison, Mahaska, Story, and Van Buren counties.

KANSAS: Brown, Cherokee, Johnson, Labette, Miami, Wallace, and Wyandotte counties.

KENTUCKY: Boyd, Caldwell, Campbell, Fleming, McCracken, Powell, Pulaski, Union, and Warren counties.

MASSACHUSETTS: Bristol, Essex, Middlesex, Norfolk, Suffolk, and Worcester counties.

MICHIGAN: Cass, Ingham, Jackson, Kent, and St. Clair counties.

MISSOURI: Boone, Butler, Callaway, Cass, Christian, Clay, Dade, Dallas, Dent, Dunklin, Franklin, Greene, Jackson, Jasper, Jefferson, Johnson, Linn, McDonald, Macon, Madison, Marion, Morgan, Nodaway, Phelps, Pike, Pulaski, St. Clair St. Francois, St. Louis, Scotland, Shannon, and Stone counties.

NEW HAMPSHIRE: Hillsborough County.

NEW YORK: Bronx, Rockland, and Suffolk counties.

NEW JERSEY: Burlington, Camden, Cape May, Essex, Gloucester, Salem, Somerset, Sussex, and Union counties.

OHIO: Adams, Allen, Athens, Auglaize, Butler, Carroll, Champaign, Clark, Coshocton, Defiance, Fairfield, Fulton, Gallia, Hamilton, Hocking, Jackson, Lake, Lucas, Marion, Madison, Meigs, Paulding, Pickaway, Portage, Ross, Scioto, Stark, Summit, Vinton, Warren, and Wyandotte counties.

OKLAHOMA: McCurtain County.

PENNSYLVANIA: Bucks, Chester, Delaware, Lancaster, Northampton, and Schuylkill counties.

RHODE ISLAND: Providence County.

VIRGINIA: Dinwiddie, Greensville, James City, Nansemond, Shenandoah, Sussex, and York counties.

46. ASCLEPIAS HALLII A. Gray, in Proc. Amer. Acad. 12:69. 1877. [T.: *E. Hall 480*, MO!]

Asclepias curvipes A. Nels. in Bull. Torrey Bot. Club 28:299. 1901. [T.: *Nelson 1656*, MO!]

Asclepias lonchophylla Greene, Leafl. Bot. Obs. & Crit. 2:231. 1912. [T.: *Purpus s. n.*, MO!]

Herbaceous perennials. Stems usually relatively slender, usually simple but occasionally sparingly branched toward the base, 2–5 dm. tall, densely and minutely puberulent to glabrate. Leaves irregularly approximate, shortly petiolate, ovate to broadly lanceolate, apex acute to obtuse, base obtuse to rounded, 5–15 cm. long, 1.5–4.0 cm. broad, firmly membranaceous, somewhat glaucous, minutely and generally puberulent, particularly beneath; petioles 0.6–1.5 cm. long. Inflorescences lateral and solitary at few to several of the upper nodes, several- to many-flowered; peduncles minutely puberulent, 1–5 cm. long; pedicels more slender, minutely puberulent, 1.5–2.5 cm. long. Flowers rather large; calyx lobes lanceolate, about 3 mm. long, minutely puberulent; corolla reflexed-rotate, rather pale livid rose or

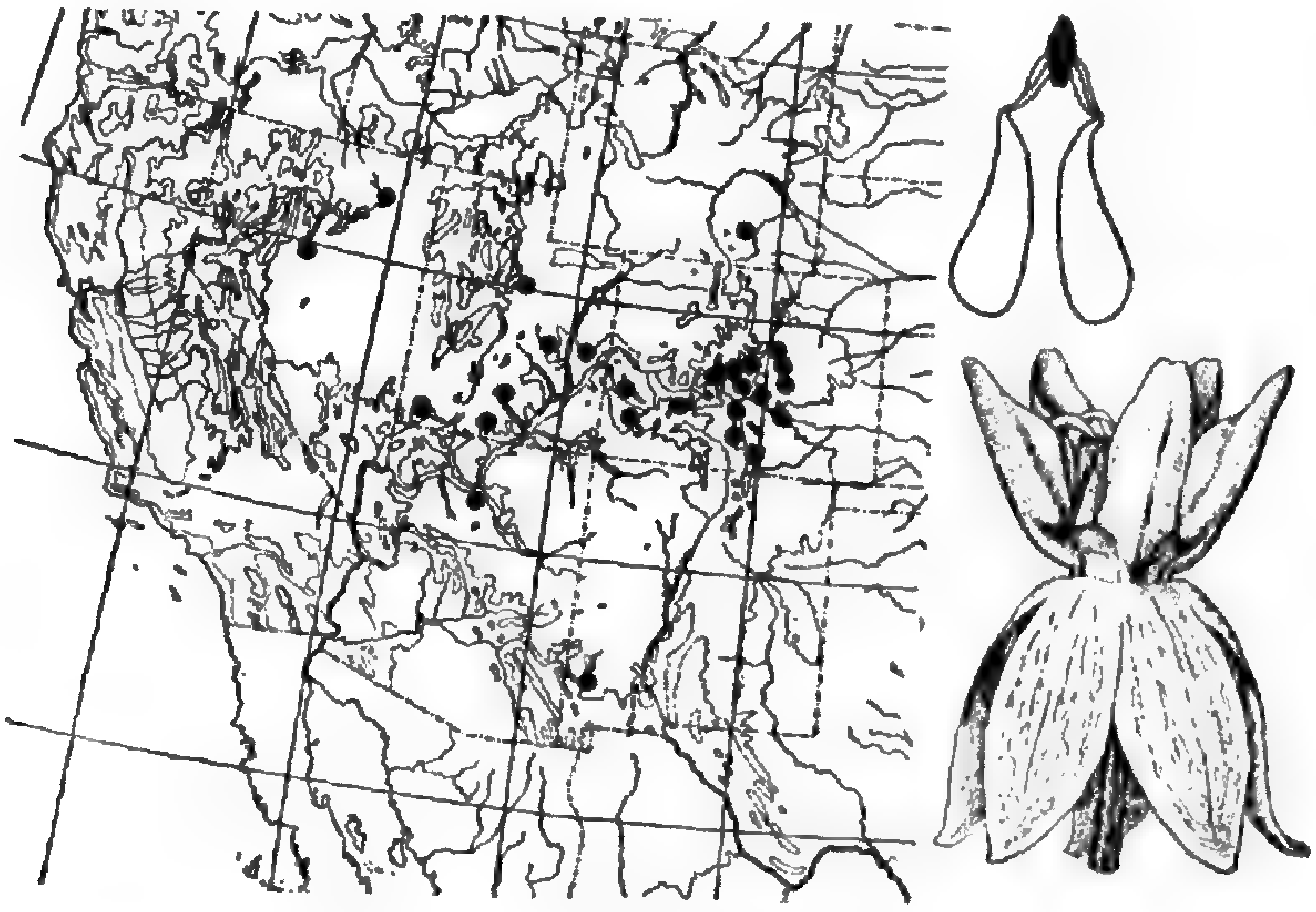

Fig. 52. *Asclepias hallii* A. Gray

purple, the lobes 6–8 mm. long; gynostegium pale rose to cream, shortly stipitate, the column obconic, about 1 mm. long and 1.5 mm. broad, the hoods oblong-elliptic, acute, 4.5–5.0 mm. long, the horn adnate about the middle, falciform, abruptly incurved, shorter than the hood, the anther head truncately conic, about 2 mm. long and 3 mm. broad. Follicles erect on deflexed pedicels, rather broadly fusiform and shortly apiculate, 8–12 cm. long, 1–3 cm. broad, smooth, minutely puberulent to glabrate; seeds broadly oval, about 7 mm. long, the white coma about 3.5 cm. long.

Stony slopes with pinyon and juniper, sagebrush, or yellow pine, sometimes spreading to roadsides. Wyoming and Colorado to Nevada and northern Arizona. Blooming from June to August.

United States:
arizona: Coconino County.
colorado: Chaffee, Costilla, Denver, Douglas, El Paso, Fremont, Gunnison, Jefferson, Lake, Montrose, Ouray, Park, Pueblo, Rio Grande, Saguache, and San Miguel counties.
nevada: Elko and Lander counties.
new mexico: Grant County.
utah: Emery, Garfield, Grand, Kane, Utah, and Washington counties.
wyoming: Albany County.

47. **Asclepias lanuginosa** HBK. Nov. Gen. 3:193. 1819. [T.: *Bonpland 4056*, MO, photo!]

Asclepias otarioides Fourn. in Ann. Sci. Nat. Bot. Ser. VI, 14:373. 1882, ex char. [T.: *Uhde 733*.]
Asclepias scheryi Woodson, in Ann. Missouri Bot. Gard. 28:285. 1941. [T.: *Schery 167*, MO!]

Herbaceous perennials. Stems stout, simple, 8–12 dm. tall, densely white-tomentose when young, becoming glabrate. Leaves opposite, sessile, very broadly ovate or oval to oblong, apex very broadly obtuse to rounded, base broadly cordate

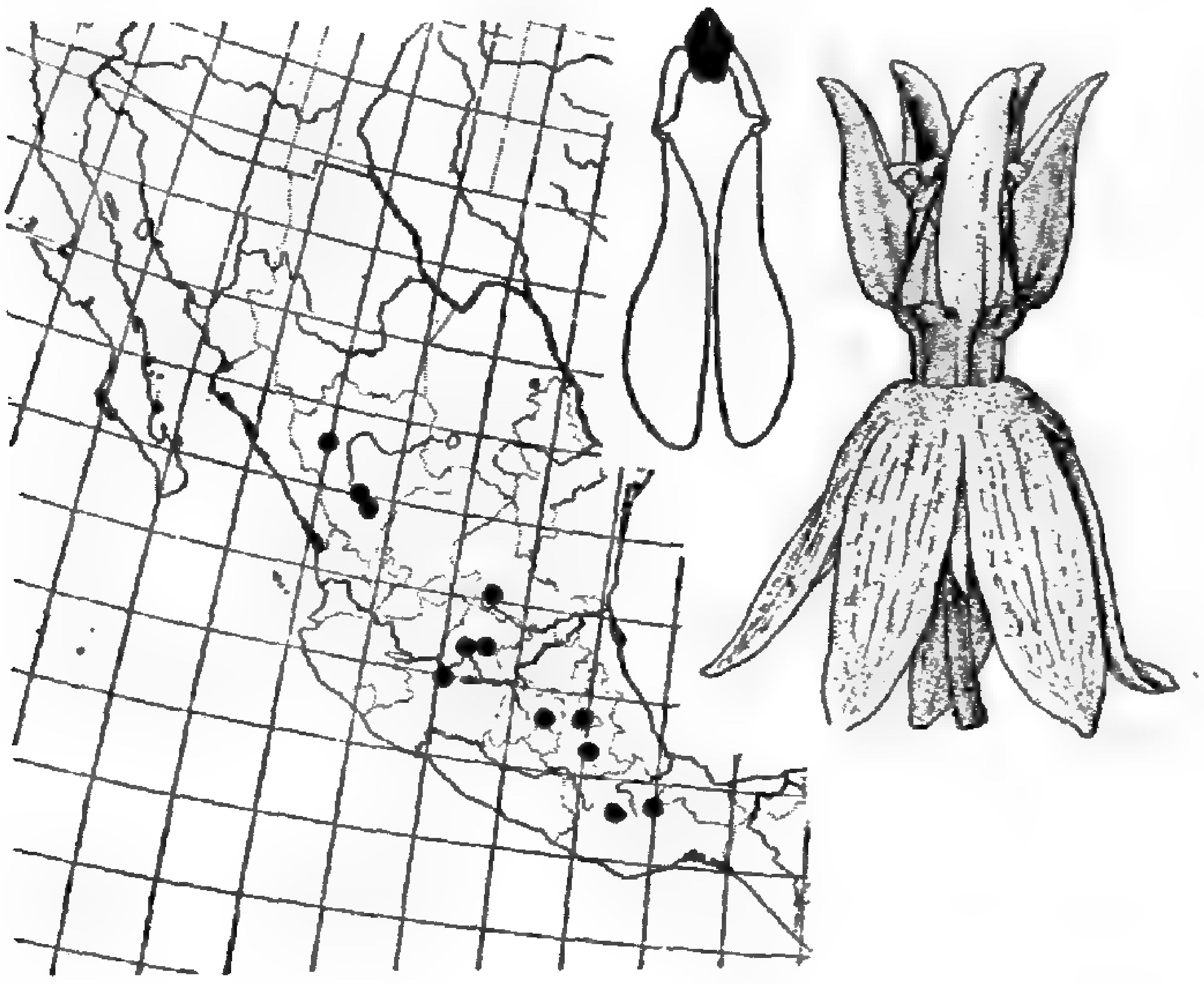

Fig. 53. *Asclepias lanuginosa* HBK.

and amplexicaul (shortly petiolate and rounded in certain putative hybrids), 10–20 cm. long, 6–14 cm. broad, firmly membranaceous, dark green and glabrate above, paler and densely white-tomentose beneath (glabrous or nearly so in certain putative hybrids). Inflorescences solitary and lateral at few to several of the uppermost nodes, usually many-flowered; peduncles rather stout, 3–10 cm. long, softly tomentose; pedicels more slender, 2–3 cm. long, tomentulose. Flowers large and showy; calyx lobes lanceolate, about 6 mm. long, minutely tomentulose or puberulent, purple; corolla reflexed-rotate, purplish rose, sometimes greenish within, the lobes 8–9 mm. long; gynostegium pale purplish to cream, shortly stipitate, the column obconic, 1.5–2.0 mm. long, 2.5–3.0 mm. broad, the hoods ovate-lanceolate, acuminate, 6–8 mm. long, the horn adnate to about the middle, rather narrowly falciform and gradually incurved, about as long as the hood, the anther head rather narrowly truncate-conic, about 2.5 mm. long and 3.0–3.5 mm. broad. Follicles erect on deflexed pedicels, rather narrowly fusiform, gradually apiculate, 10–13 cm. long, about 1.5–2.0 cm. broad, rather sparsely white-tomentose to glabrate; seeds oval, about 6 mm. long, the white coma about 4 cm. long.

Mountain slopes, sparsely wooded grassland, open places in pine and oak woods, lava beds. South-central Mexico. Blooming from June to August.

MEXICO: DURANGO: Otinapa, Indé, Coyotes Hacienda, Arroyo Mimbres. DISTRITO FEDERAL: Eslava, Valley of Mexico. GUANAJUATO: Santa Rosa. MICHOACAN: Pátzcuaro. OAXACA: Sierra de San Felipe, Montelobos, Nochixtlán, Etla. PUEBLA: Cerro de Chicamola, San Luis. SAN LUIS POTOSÍ: Alvarez, San Luis Potosí. TLAXCALA: Tlaxcala.

Dugès reports the popular name of *taraumara.*

Typical *A. lanuginosa* is quite unlike any other Mexican milkweed, with its broad leaves densely white-tomentose beneath, and its handsome purplish rose flowers. However, many specimens in our herbarium collections which are quite obviously of the same species have large but proportionately narrower leaves definitely petiolate and scarcely if at all cordate, and flowers that are frequently somewhat smaller as well; still others have conspicuously smaller and paler flowers and smaller, less conspicuouly tomentose leaves. One specimen of the latter series (*Schery 167*) has the smaller flowers combined with deeply cordate and amplexicaul leaves of the type of true *A. lanuginosa*, but virtually glabrous or only inconspicuously puberulent beneath.

Such evidence leads me to suppose that *A. lanuginosa* hybridizes quite frequently with some neighboring species, of which the most likely candidate appears to be either *A. ovata* or *A. pringlei.*

Although superficially rather similar because of their rather small, inconspicuously puberulent leaves and crowded smallish flowers, *A. ovata* and *A. pringlei* are very easy to tell apart: *A. ovata* by its long narrow column, long anther head, and shortly stipitate hoods with slender horns; *A. pringlei* by its very short column, short and broad anther head, and conspicuously stipitate hoods with very short horns, if any. Both species occur within the range of *A. lanuginosa,* which, because of its rather narrow column and anther head, might also be placed as well in the series TUBEROSAE as in the PURPURASCENTES (I have placed it in the latter because of the absence of marginal auricles to the hoods).

Asclepias pringlei might appear to be a poor candidate for hybridization with *A. lanuginosa* not only because of its column and anther heads which are proportionally less like the latter species than those of *A. ovata,* but particularly because of its peculiar pendulous follicles with naked seeds. Nevertheless, an examination of the putative hybrids definitely shows a strong tendency for both the column and the hood to be short and squat much more in the manner of *pringlei* than of *ovata,* and I have been driven rather reluctantly to the conclusion that the putative hybrids most likely are products of cross pollination of *A. lanuginosa* × *pringlei,* and I am labelling the herbarium specimens as such.

Here, again, one is bound to question the close analysis of floral structures (or fruiting for that matter) as clues to true natural relationships in the asclepiads, and to doubt whether a trustworthy phylogeny of the family can ever be reconstructed.

Unfortunately, the type specimen of *A. lanuginosa* is one of the putative hybrids. The supposedly homozygous population is represented by Fournier's description of *A. otarioides,* the type specimen of which was said by him to be deposited at Berlin and hence is supposedly lost. Most of the putative hybrids in our herbarium collections have been determined previously as *A. ovata,* which they indeed approach in superficial appearance except for the somewhat larger flowers and leaves (although the gynostegia are quite different as has already been discussed). The type specimen of *A. scheryi* is of particular interest since it approaches *A. pringlei* so closely in the flowers and *A. lanuginosa* in the leaves (except for the lack of the characteristic tomentum).

48. **Asclepias curtissii** A. Gray, in Proc. Amer. Acad. 19:85. 1883. [T.: *Curtiss s. n.*, MO!]

Asclepias aceratoides Nash, in Bull. Torrey Bot. Club 22:154. 1895, non M. A. Curtis. [T.: *Nash 1092*, MO!]
Asclepias arenicola Nash, loc. cit. 23:252. 1896. [Based on *A. aceratoides* Nash, non M. A. Curtis.]
Oxypteryx arenicola (Nash) Greene, in Pittonia 3:235. 1897.
Oxypteryx curtissii (A. Gray) Small, Man. Southeast. Fl. 1072. 1933.

Decumbent herbaceous perennials from fleshy fusiform rootstalks. Stems relatively slender, simple or branching sparingly, 3–7 dm. long, inconspicuously puberulent to glabrate. Leaves opposite, petiolate, broadly oval or ovate and almost quadrate, apex broadly obtuse to broadly rounded and more or less retuse with a short mucro, base broadly rounded, 2–5 cm. long, 1.5–3.0 cm. broad, firmly membranaceous, glabrous; petioles 4–7 mm. long. Inflorescences solitary and lateral at few to several of the uppermost nodes, rather many-flowered; peduncles rather slender, 2.5–4.0 cm. long, finely puberulent; pedicels slender, 1.0–1.5 cm. long, minutely puberulent. Flowers rather small; calyx lobes narrowly lanceolate, 2.5–3.0 mm. long; corolla reflexed-rotate, pale green or greenish white, the lobes about 6 mm. long; gynostegium subsessile, white or cream, the column very broadly obconic, about 0.5 mm. long and 2 mm. broad, the hoods oblong-lanceolate, narrowly acute, 4.5–5.0 mm. long, the horn about half adnate, falciform and sharply incurved, much shorter than the hoods, the anther head very broadly truncate-conic, about 1.5 mm. long and 3 mm. broad. Follicles unknown.

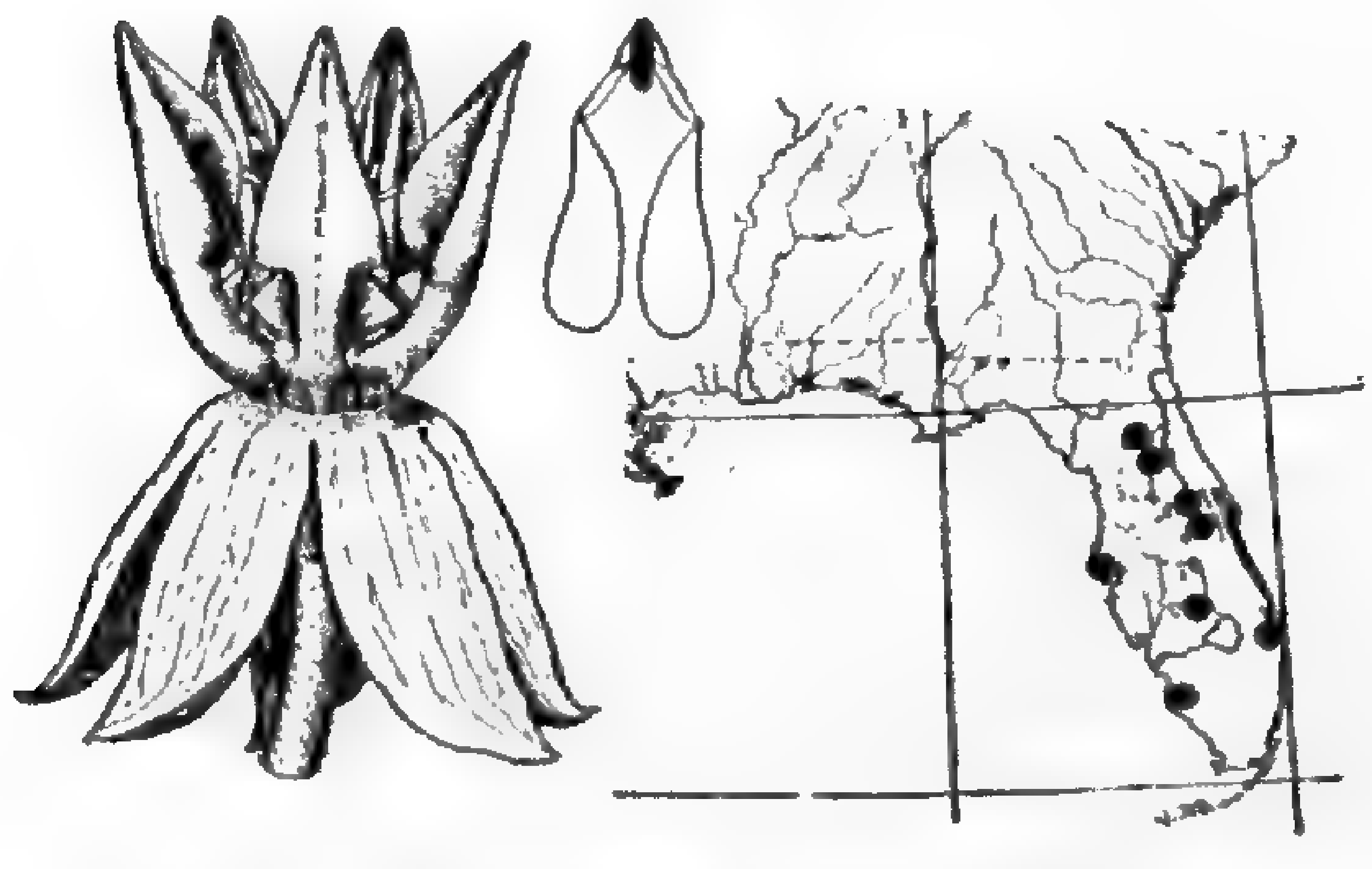

Fig. 54. *Asclepias curtissii* A. Gray

Dry sandy scrub and pinelands. Southern Florida. Blooming from April to August.

United States:
florida: Brevard, Collier, De Soto, Highlands, Lake, Marion, Orange, Osceola, Palm Beach, and Pinellas counties.

A most peculiar little species rather resembling a white-flowered *A. tuberosa* at a casual glance. Definitely of the affinity of *A. purpurascens*, however.

49. **Asclepias speciosa** Torr. in Ann. Lyc. N. Y. 2:218. 1828, ex char. [T.: *James 258*.]

Asclepias douglasii Hook. Fl. Bor.-Amer. 2:53, *t. 142*. 1840, ex ic.

Herbaceous perennials. Stems usually very stout, simple, 6–10 dm. tall, densely white-tomentose generally. Leaves opposite, shortly petiolate, broadly ovate or oval to rather narrowly oblong or ovate-lanceolate, apex usually very broadly obtuse to rounded, rather rarely acute, base very broadly obtuse to rounded and sometimes broadly and shallowly cordate, 6–20 cm. long, 3–14 cm. broad, firmly membra-

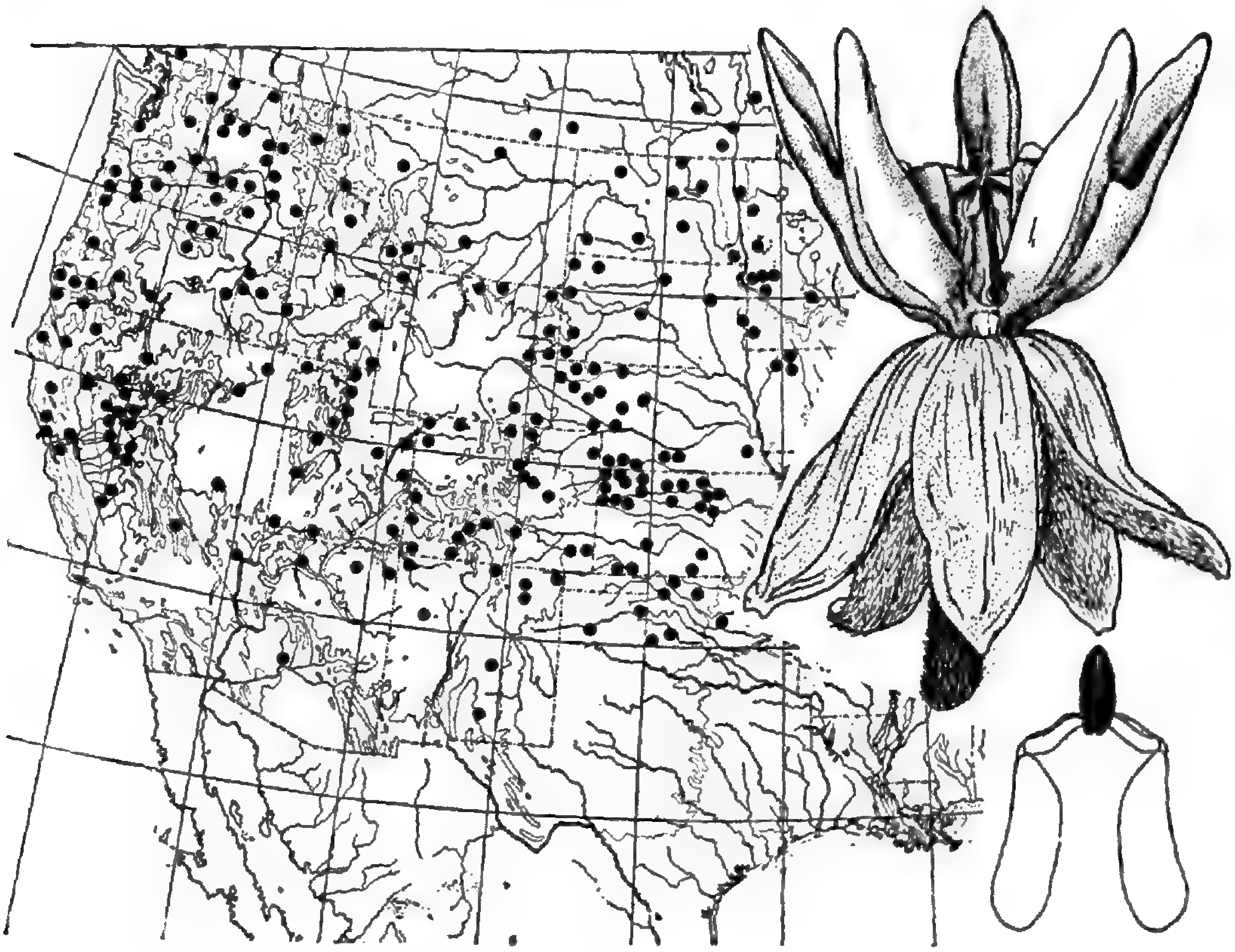

Fig. 55. *Asclepias speciosa* Torr.

naceous, very densely white-tomentose beneath, more or less glabrate above; petioles 0.5–1.5 cm. long. Inflorescences lateral and solitary at few to several of the upper nodes, several- to many-flowered, densely white-tomentose throughout; peduncles rather stout, 1–10 cm. long; pedicels 2–3 cm. long. Flowers very large and showy; calyx lobes lanceolate, 5–6 mm. long, very densely white-tomentose; corolla purplish rose, the lobes 10–15 mm. long; gynostegium pale rose or pinkish cream, subsessile, the column very broadly obconic, about 1 mm. long and 3 mm. broad, the hoods very narrowly ovate-lanceolate, gradually attenuate, widely spreading, 10–14 mm. long, the horn adnate toward the base, falciform-acicular, sharply incurved, very much shorter than the hoods, the anther head broadly truncate-conic, about 3 mm. long and 4.5 mm. broad. Follicles erect on deflexed pedicels, broadly or rather narrowly fusiform, abruptly or gradually attenuate, 9–12 cm. long, 2–3 cm. broad, densely spiny to smooth, very densely white-tomentose; seeds oval, 6–9 mm. long, the white coma 3–4 cm. broad.

Widely tolerant to habitat and becoming weedy in cultivated fields, roadsides, and railways. Southern Manitoba to British Columbia; Minnesota to northwestern Texas and westward to the Pacific Coast. Blooming from May to September.

CANADA: MANITOBA: Gladstone, Lakeside, Morden, and Winnipeg. SASKATCHEWAN: Maple Creek and Willow Bunch. BRITISH COLUMBIA: Kimberly.

UNITED STATES:

ARIZONA: Apache, Coconino, Maricopa, and Navajo counties.

CALIFORNIA: Amador, Butte, Calaveras, Contra Costa, Del Norte, Eldorado, Fresno, Humboldt, Inyo, Lake, Marin, Mariposa, Mono, Nevada, Placer, Plumas, Shasta, Sierra, Solano, Siskiyou, Sonoma, Trinity, and Tuolumne counties.

COLORADO: Archuleta, Bent, Boulder, Denver, Elbert, El Paso, Fremont, Jefferson, Larimer, Mesa, Mineral, Moffatt, Montezuma, Montrose, Prowers, Rio Blanco, Routt, Saguache, Weld, and Yuma counties.

IDAHO: Ada, Bannock, Butte, Bonneville, Canyon, Goodding, Idaho, Kootenai, Latah, Lemhi, Nez Perce, and Payette counties.

KANSAS: Cheyenne, Clay, Cloud, Decatur, Ellis, Gove, Graham, Harper, Harvey, Logan, Meade, Norton, Osborne, Ottawa, Pawnee, Rawlins, Riley, Rooks, Saline, Seward, Sheridan, Sherman, and Wallace counties.

IOWA: Clay, Emmet, and Palo Alto counties.

MINNESOTA: Big Stone, Chippewa, Hennepin, Kandiyohi, Mahnomen, Otter Tail, Pipestone, Polk, and Swift counties.

MONTANA: Deer Lodge, Flathead, Gallatin, Lewis and Clark, Missoula, Park, Phillips, Sanders, and Yellowstone counties.

NEBRASKA: Box Butte, Cherry, Cheyenne, Custer, Dawes, Deuel, Dundy, Garden, Grant, Kearney, Lancaster, Lincoln, Phelps, Red Willow, Sheridan, Sioux, and Thomas counties.

NEVADA: Churchill, Clark, Douglas, Elko, Eureka, Nye, Story, and Washoe counties.

NEW MEXICO: Lincoln, Mora, Otero, San Juan, San Miguel, Taos, Union, and Valencia counties.

NORTH DAKOTA: Benson, Morton, Ramsey, Richland, Stutman, Slope, Towner, and Ward counties.

OKLAHOMA: Beckham, Major, Oklahoma, Washita, Woods, and Woodward counties.

OREGON: Benton, Clackamas, Crook, Curry, Grant, Hood River, Jackson, Josephine, Klamath, Lake, Lane, Malheur, Marion, Polk, Umatilla, Union, Wheeler, and Yamhill counties.

SOUTH DAKOTA: Brookings, Butte, Fall River, Harding, Pennington, Perkins, Spink, Stanley, and Walworth counties.

TEXAS: Hemphill and Randall counties.

UTAH: Box Elder, Cache, Carbon, Grand, Juab, Kane, Millard, Salt Lake, San Juan, Uintah, Utah, and Washington counties.

WASHINGTON: Benton, Chelan, Columbia, Douglas, Grant, Kittitas, Lincoln, Okanogan, Skamania, Stevens, Spokane, Thurston, Walla Walla, Whitman, and Yakima counties.

WYOMING: Albany, Bighorn, Converse, Crook, Laramie, Niobrara, Sheridan, Weston, and Yellowstone counties.

Asclepias speciosa bears the most massive flowers of the American milkweeds and the inflorescences are quite handsome when studied individually, in spite of lack of a clear color. Nevertheless, the plants are rather weedy and not likely to be cultivated. In Minnesota, Iowa, and the Dakotas occasional spontaneous hybrids with *A. syriaca* are found, and the cross has been performed experimentally by Prof. O. A. Stevens, of the North Dakota Experiment Station. As has already been discussed under *A. syriaca*, a broad east-west cline exists in *A. speciosa* with respect to the follicles, which tend to be conspicuously spiny in the east and smooth in the west; a complementary cline is found in *A. syriaca*.

50. **ASCLEPIAS EUPHORBIAEFOLIA** Engelm. ex A. Gray, in Proc. Amer. Acad. 16:104. 1881. [T.: *Schaffner 55*, MO!]

Small prostrate herbaceous perennials. Stems very slender, simple, clustered from the rootstalk, 5–9 cm. long, very minutely puberulent. Leaves opposite, petiolate, very broadly ovate, suborbicular, apex very broadly obtuse to rounded, base broadly rounded, 4–9 mm. long, 4–5 mm. broad, subsucculent, glabrous; petioles 1–2 mm. long. Inflorescences subterminal from 1 to few uppermost nodes, few-flowered; peduncle slender, 1–2 cm. long or nearly sessile, minutely puberulent; pedicels very slender, about 1 cm. long. Flowers small; calyx lobes ovate, about 2 mm. long; corolla pale pink, the lobes about 4 mm. long; gynostegium subsessile, pale pinkish cream, the column broadly obconic, about 1 mm. long and 1.5 mm. broad, the hoods oblong-elliptic, spreading, about 3 mm. long, the horn adnate about midway, falciform and incurved, shorter than the hood, the anther head truncately conic, about 1 mm. long and 2.5 mm. broad. Follicles erect on deflexed pedicels, narrowly fusiform, long-apiculate, about 3 cm. long and 5 mm. thick, smooth, very minutely and sparsely pilosulose; seeds unknown.

Dry, open, rocky woodlands of oak, pine, and arbutus; in sandy soil. Durango and San Luis Potosí. Blooming in July and August.

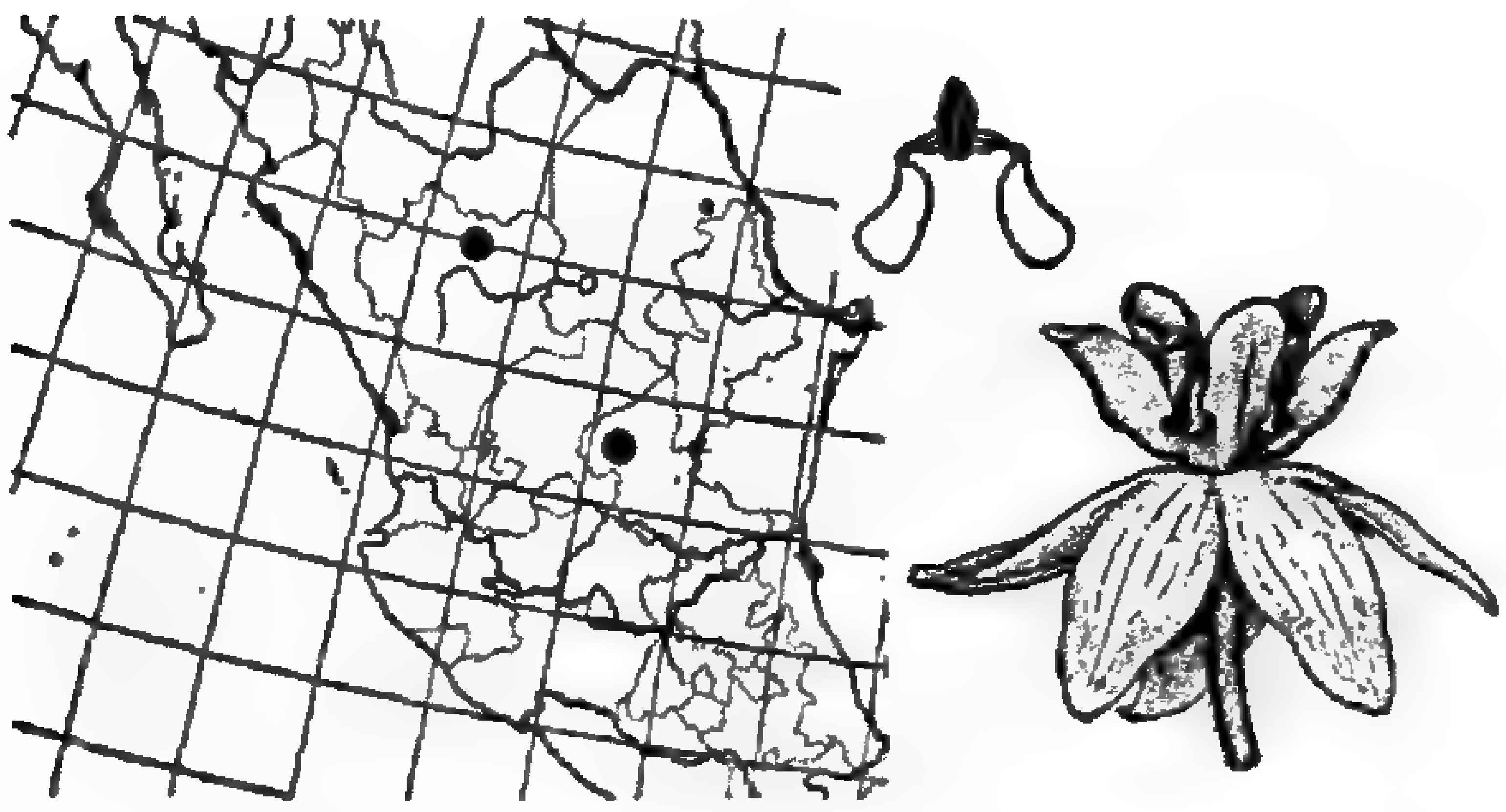

Fig. 56. *Asclepias euphorbiaefolia* Engelm.

MEXICO: DURANGO: Cerro Prieto. SAN LUIS POTOSÍ: San Miguelito.

Only four collections of *A. euphorbiaefolia* are known, three from San Luis Potosí (Schaffner in 1876 and 1879, Parry & Palmer in 1878), and the last from Durango (James H. Maysilles in 1950). Mr. Maysilles' notes are of particular interest therefore: "Rare; only 1 mat seen; plants were lying flat on ground; flowers looked like pink cloverbloom from a distance of 2 meters away."

Series 7. MACROTIDES

KEY TO THE SPECIES

a. Flowers relatively small, the corolla lobes about 4–8 mm. long, greenish white more or less suffused with purple.

b. Leaves irregularly approximate.

c. Inflorescence pedunculate or infrequently subtended by a reduced leaf; leaves rather uniformly linear to filiform.

d. Inflorescences typically terminal and solitary, rather long-pedunculate; follicles erect on erect pedicels. Coastal Plain from South Carolina to Louisiana....51. *A. michauxii*

dd. Inflorescences lateral at several upper nodes, very shortly pedunculate; follicles known. Oaxaca ....52. *A. conzattii*

cc. Inflorescences sessile and typically subtended by few to several leaves; leaves variable, broadly ovate to narrowly lanceolate.

d. Plants inconspicuously puberulent; leaves lanceolate; hoods about twice as long as the anther head. New Mexico and adjacent Kansas and Colorado to southern Arizona and southward to Coahuila and Durango........................53. *A. involucrata*

dd. Plants conspicuously tomentulose; leaves broadly ovate to ovate-lanceolate; hoods barely longer than the anther head. Southern Utah and northern Arizona..54. *A. macrosperma*

bb. Leaves opposite.

c. Leaves ovate to narrowly lanceolate, abruptly cuneate; hoods rather obtuse, barely longer than the anther head; small herbs. San Luis Potosí and Hidalgo........55. *A. puberula*
cc. Leaves filiform to acicular; hoods narrowly acuminate, about three times as long as the anther head; plants suffrutescent. Western Texas to southern New Mexico and Arizona; Coahuila ....56. *A. macrotis*
aa. Flowers relatively large, the corolla lobes about 1 cm. long.
b. Plants very stout, conspicuously setose-pilose generally; leaves very broadly and regularly oval, subsessile, cordate and rather amplexicaul; flowers very many and crowded, pale green. Southern Arizona; Chihuahua to Sonora and southward to Jalisco....57. *A. lemmoni*
bb. Plants more slender, inconspicuously puberulent to glabrate; leaves broadly ovate to ovate-lanceolate, obtuse to rounded at the base, distinctly petiolate; flowers rather few and lax, deep purple. Oaxaca ....58. *A. laxiflora*

51. Asclepias michauxii Dcne. in DC. Prodr. 8:569. 1844, ex char. [T.: *Michaux s. n.*]

Asclepias angustifolia Ell. Sketch Bot. South Car. & Ga. 1:325. 1821. [T.: Elliot Herb., Charleston Mus., GH photo!]
Oligoron tenuifolium Raf. New Fl. North Amer. 4:60. 1838, ex char.

Herbaceous perennials from rather fleshy, subfusiform rootstalks. Stems slender, simple or sparingly branched from the base, decumbent or ascending, 1–4 dm. long, minutely and rather sparsely pilosulose to glabrate. Leaves irregularly approximate, sessile, linear to filiform, 3–12 cm. long, 1–6 mm. broad, firmly membranaceous and frequently somewhat revolute, very minutely and sparsely pilosulose to essentially glabrous. Inflorescences terminal and solitary or very rarely lateral also at the uppermost node, usually long-pedunculate but rarely immediately subtended by a reduced leaf, several- to many-flowered; peduncles 3–6 cm. long, rarely absent; pedicels slender, 0.9–1.3 cm. long, very minutely and scatteringly pilosulose. Flowers rather mediocre; calyx lobes lanceolate, 2.5–4.0 mm. long; corolla reflexed, rotate, greenish white and usually more or less suffused with purple without, the lobes 4–6 mm. long; gynostegium stipitate, white, the column obconic, about 1 mm. long and 1.5 mm. broad, the hoods ovate, acute, 2–4 mm. long, the horn adnate toward the base, falciform and incurved, about as long as the hood, the anther head truncately conic, about 1.5 mm. long and 2 mm. broad. Follicles erect on erect pedicels, very narrowly fusiform, long-attenuate, 10–15 cm. long, 5–8 mm. broad, smooth, essentially glabrous; seeds broadly oval, about 8 mm. long, the white coma 4.0–4.5 cm. long.

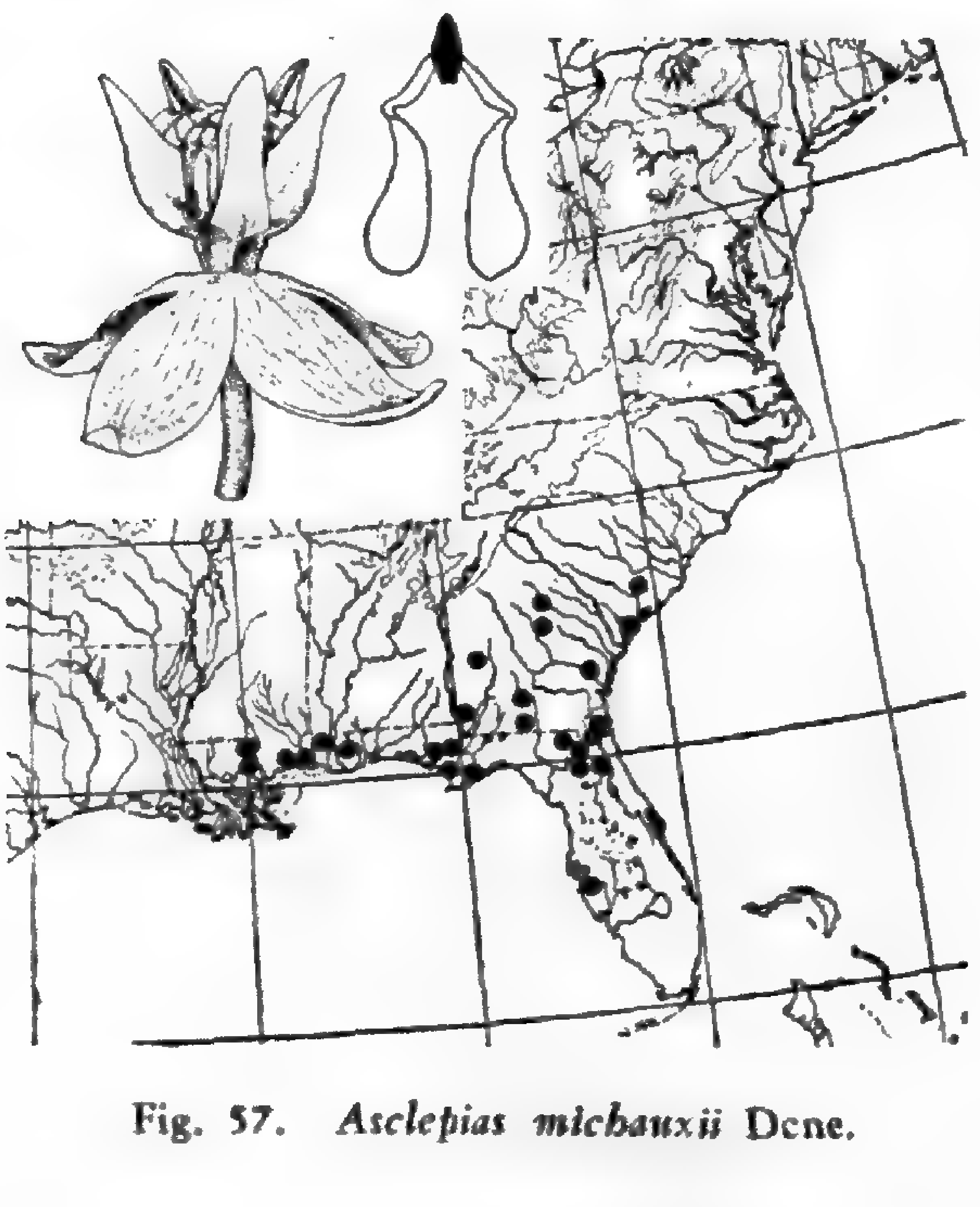
Fig. 57. *Asclepias michauxii* Dcne.

Sandy pine barrens. South Carolina to Florida and westward to Louisiana. Blooming from April to June.

UNITED STATES:
ALABAMA: Baldwin and Mobile counties.
FLORIDA: Alachua, Baker, Bay, Bradford, Calhoun, Clay, Columbia, Duval, Franklin, Gulf, Manatee, Nassau, and Putnam counties.
GEORGIA: Berrien, Early, Laurens, Lowndes, Sumter, Wayne, and Washington counties.
LOUISIANA: St. Tammany and Washington parishes.
MISSISSIPPI: Harrison, Jackson, and Yalobusha counties.
SOUTH CAROLINA: Beaufort and Dorchester counties.

I have tried to include *A. michauxii* with the INCARNATAE because of the follicles erect on erect pedicels; but the structure of the gynostegium definitely allies it with the MACROTIDES, particularly with two geographically and environmentally distant species, *A. involucrata* and *A. macrosperma,* both of which also have approximately scattered leaves but with follicles erect on deflexed pedicels.

52. ASCLEPIAS **conzattii** Woodson, spec. nov.

Herbae perennes an suffrutices. Caules graciles sublignosi altitudine ignoti aliquando compositi glabri vel juventate sparse minutissimeque pilosuli. Folia sat densa irregulariter approximata sessilia filiformia 8–13 cm. longa ca. 2 mm. lata revoluta glabra. Inflorescentiae e nodis superioribus subsessiles pauciflorae; pedunculis ca. 3–5 mm. longis subnullis; pedicellis gracilibus ca. 1.5 cm. longis glabris. Flores mediocres; calycis laciniis ovato-lanceolatis 4–5 mm. longis; corolla reflexe rotata colore pallido ignoto, lobis 7–8 mm. longis; gynostegio breviter stipitato, columna obconica ca. 1 mm. longa 2 mm. lata, cucullis late ovatis acuminatis conduplicatis ca. 6 mm. longis patulis marginibus exauriculatis cornu valde adnato falciforme cucullo multo breviore, androecio truncate conico ca. 2 mm. longo 3 mm. lato. Folliculi mihi ignoti.—Holotypus: *C. Conzatti 4024* in Herb. N. Y. Bot. Gard. ("De Almoloyas a Tomellín, 800 metros. Distrito de Nochixtlán, Oaxaca, Mexico, Julio 14 de 1920.")

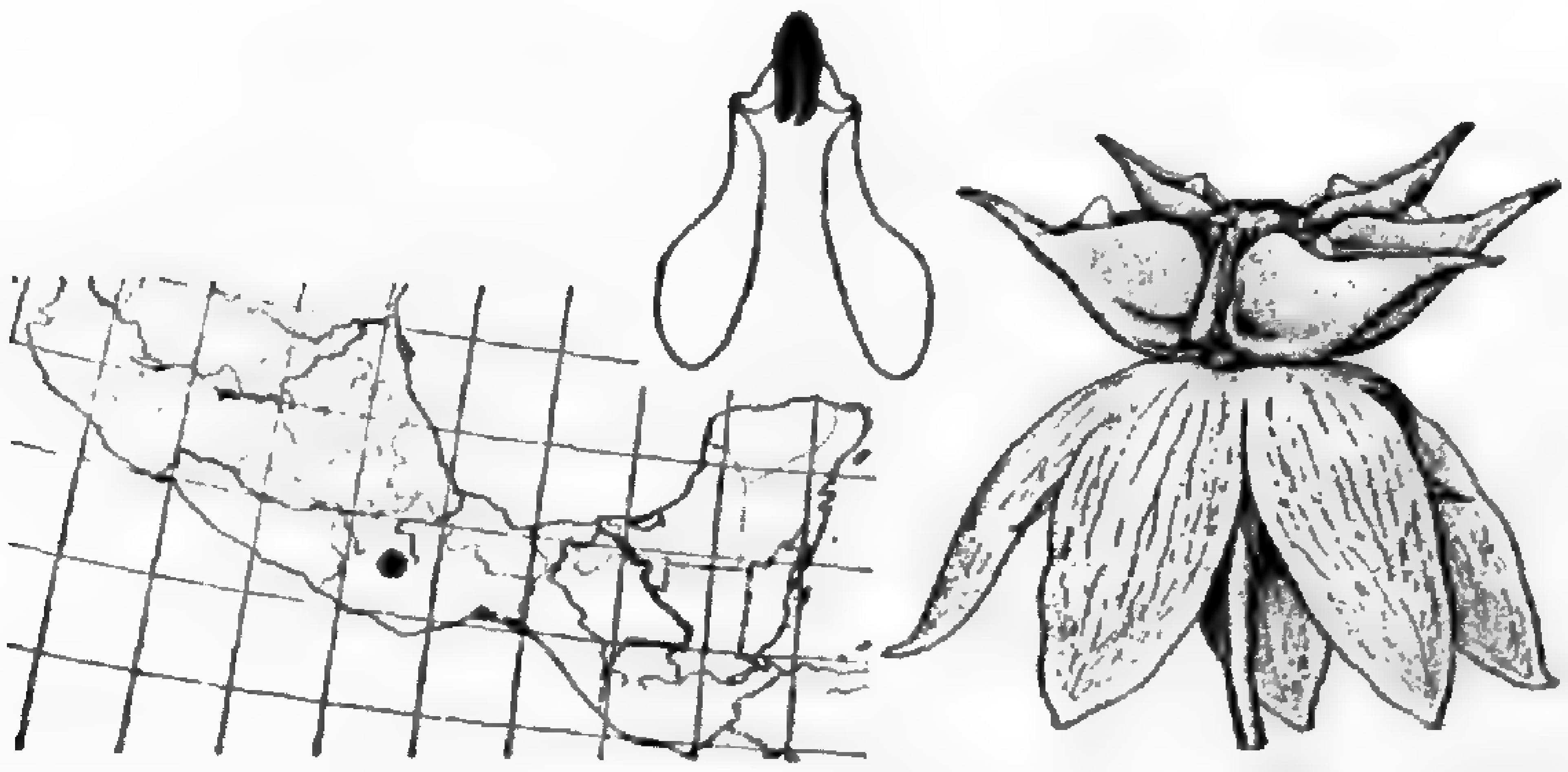

Fig. 58. *Asclepias conzattii* Woods.

The type specimen apparently does not include the entire stem, but from the several branches and the definite periderm I surmise the plant to have been suffruticose, at least. An extremely distinct species.

53. Asclepias involucrata Engelm. ex Torrey, in Bot. Mex. Bound. Surv. 163. 1859. [T.: *Wright 1690*, MO!]

Low herbaceous perennials from woody subfusiform rootstalks. Stems clustered from the rootstalk, ascending or more or less decumbent, rather slender, branching repeatedly, 3–25 cm. long, minutely and generally puberulent. Leaves irregularly approximate, sessile or subsessile, narrowly lanceolate, apex very narrowly acuminate, base acute to obtuse, 1–12 cm. long, 3–10 mm. broad, firmly membranaceous and somewhat conduplicate, inconspicuously pilosulose particularly beneath. Inflorescences terminal and usually also from the few uppermost nodes, sessile, several- to few-flowered; pedicels 1.5–2.5 cm. long, minutely puberulent. Flowers rather small; calyx lobes ovate-lanceolate, 3–4 mm. long; corolla reflexed-rotate, pale green or pink, tinged purple without, the lobes 5–7 mm. long; gynostegium shortly stipitate, white with purplish keels, the column obconic, 1.0–1.5 mm. long and 1.5–2.5 mm. broad, the hoods ovate, acute, 3–4 mm. long, the horns adnate toward the base, falciform, incurved or ascending, about as long at the hood, the anther head truncate-conic, about 2 mm. long and 3 mm. broad. Follicles erect on deflexed pedicels, stoutly fusiform, shortly apiculate, 4–7 cm. long, 1.5–2.0 cm. broad, very inconspicuously pilosulose to glabrate; seeds oval, 6–8 mm. long, the pale tawny coma 2–3 cm. long.

Dry gravelly hills, flats, chaparral, and arroyos. New Mexico and Arizona and adjacent Utah, Colorado, and Kansas; northern Mexico from Coahuila to Durango. Blooming from March to July.

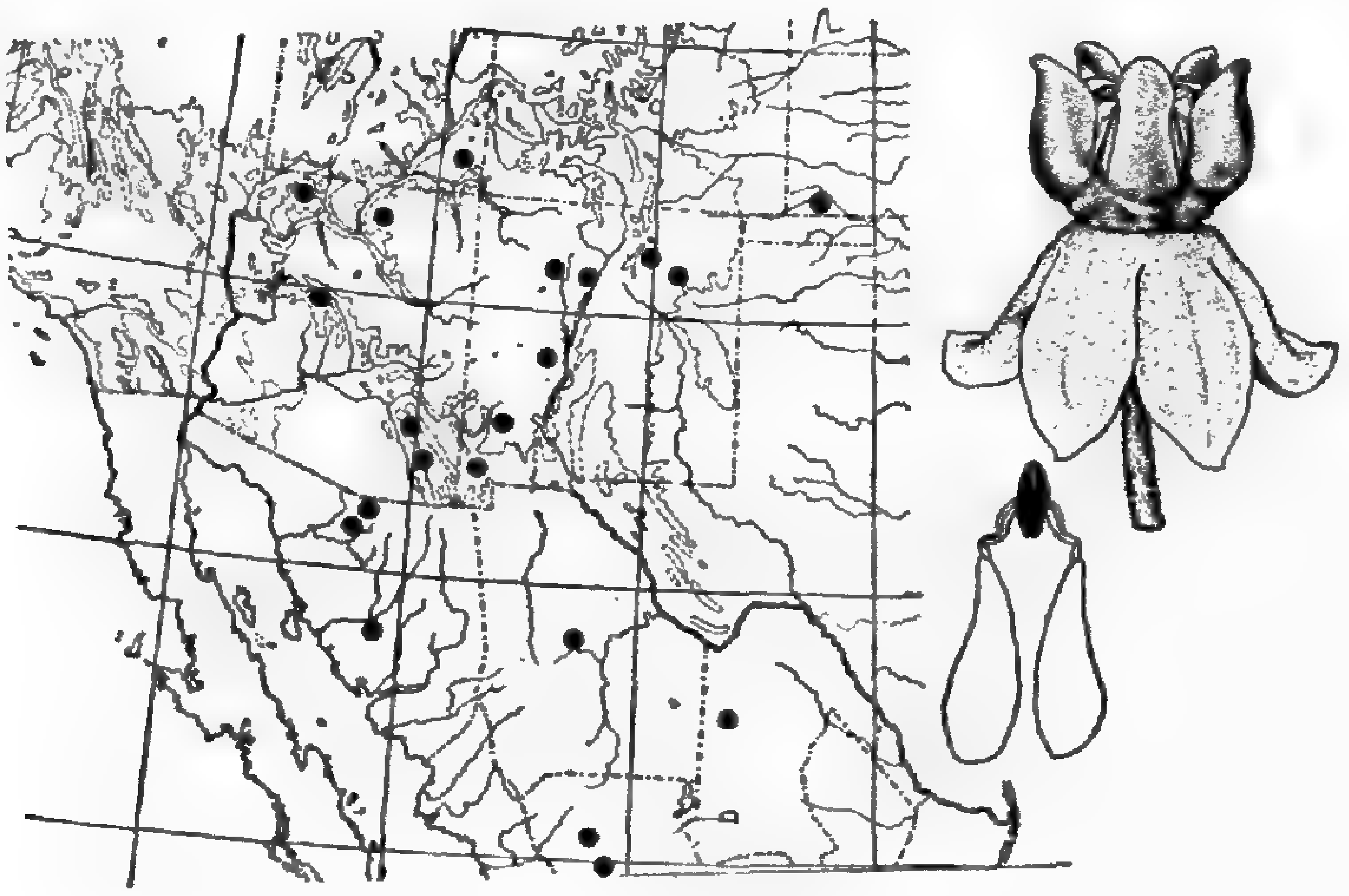

Fig. 59. *Asclepias involucrata* Engelm.

United States:

Arizona: Cochise, Coconino, Graham, Mohave, and Yavapai counties.

Colorado: Las Animas County.

Kansas: Stevens County.

New Mexico: Grant, Hidalgo, Mora, Sandoval, San Miguel, Santa Fe, and Socorro counties.

Utah: San Juan County.

Mexico: Chihuahua: Chihuahua. Coahuila: Piedras Negras. Durango: Santiago Papasquiaro, Tepehuanes. Sonora: Hermocillo, San Pedro, Nogales.

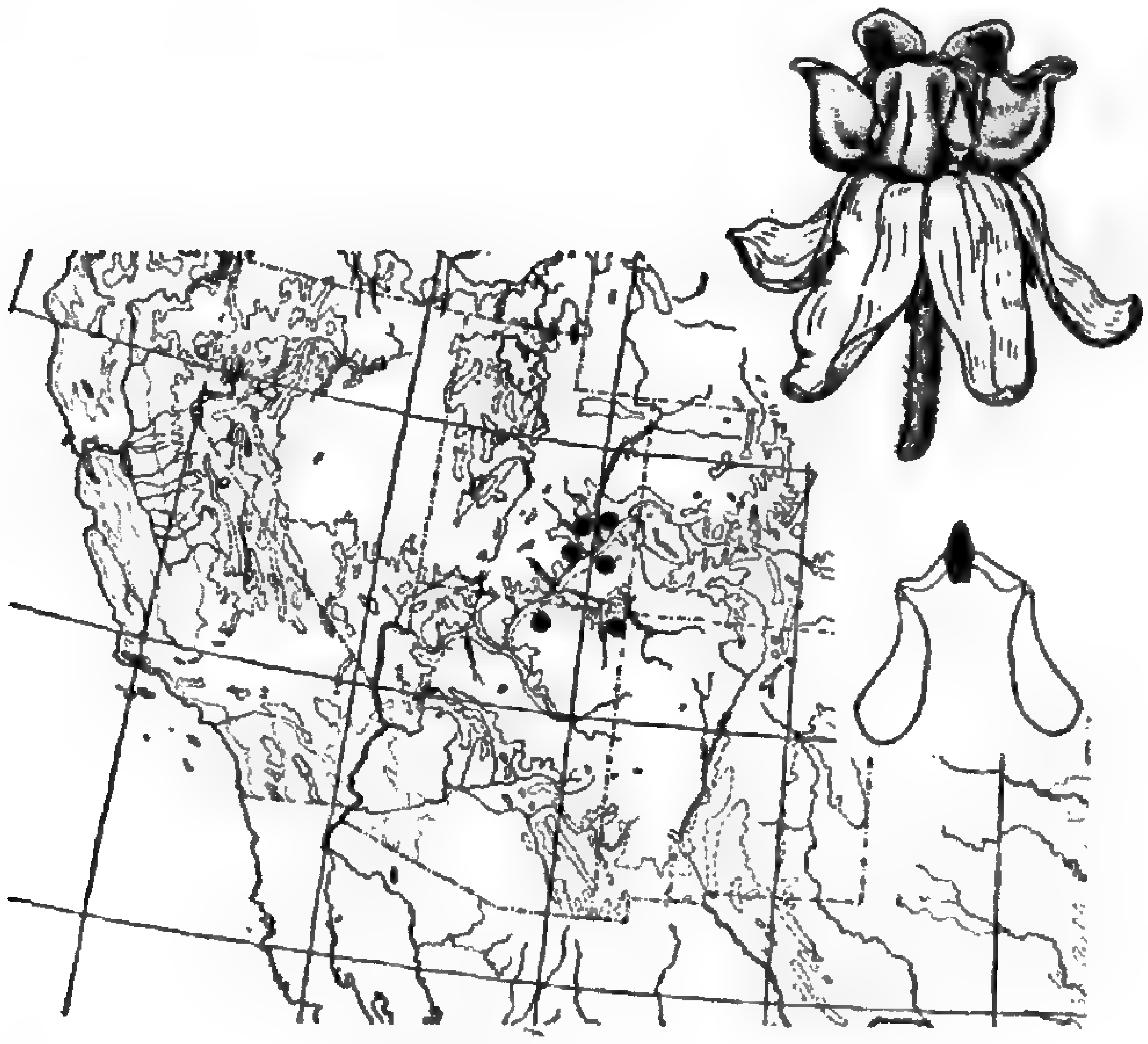

Fig. 60. *Asclepias macrosperma* Eastw.

54. ASCLEPIAS MACROSPERMA Eastw. in Bull. Torrey Bot. Club 25:172. 1898. [Based on *A. involucrata* var. *tomentosa* Eastw.]

Asclepias involucrata var. *tomentosa* Eastw. in Zoe 4:120. 1893. [T.: *Eastwood s. n.*, MO!]

Low herbaceous perennials from woody subfusiform rootstalks. Stems clustered from the rootstalk, ascending or more or less decumbent, rather stout, branching repeatedly, 4–17 cm. long, densely tomentulose. Leaves irregularly approximate, very shortly petiolate, broadly ovate to ovate-lanceolate, apex acute to obtuse, base broadly obtuse to rounded, 2–6 cm. long, 1–2 cm. broad, firmly membranaceous and somewhat crispate, densely tomentulose; petioles 1–7 mm. long. Inflorescences solitary and terminal, sessile, several- to many-flowered; pedicels rather slender, 1–2 cm. long, densely tomentulose. Flowers rather small; calyx lobes ovate, about 3 mm. long, minutely tomentulose; corolla reflexed-rotate, pale greenish more or less tinged with purple without, the lobes 5–6 mm. long; gynostegium very shortly stipitate, greenish white or cream, the column broadly obconic, about 0.7 mm. long and 1.3–1.5 mm. broad, the hoods broadly ovate, obtuse or rounded, 2.5–3.0 mm. long, the horn adnate toward the base, falciform, incurved, somewhat shorter than the hood, the anther head about 2 mm. long and 3 mm. broad. Follicles erect on deflexed pedicels, broadly fusiform, shortly apiculate, 4–6 cm. long, 1.5–2.0 cm. broad, sparsely pilosulose to glabrate; seeds very broadly oval, 1.0–1.3 cm. long, the pale tawny coma 1.3–2.0 cm. long.

Sandy soil, along washes and arroyos. Southern Utah and northern Arizona. Blooming from May to June.

UNITED STATES:
ARIZONA: Apache and Coconino counties.
UTAH: Emery, Grand, San Juan, and Wayne counties.

This species is undeniably closely related to *A. involucrata* and might be considered as a subspecies of it. But both grow together in the range of *A. macrosperma*, and I have seen no intergrading individuals.

55. ASCLEPIAS PUBERULA A. Gray, in Proc. Amer. Acad. 16:104. 1881. [T.: *Schaffner 60*, GH.]

Small herbaceous perennials from thickened subfusiform rootstalks. Stems erect or more or less decumbent, simple or weakly branched from the base, 1.5–10.0 cm. long, very inconspicuously pilosulose. Leaves opposite, rather long-petiolate, ovate to narrowly lanceolate, apex acute to narrowly acuminate, base obtuse, 2–7 cm. long, 0.5–1.5 cm. broad, membranaceous, essentially glabrous; petioles 0.5–2.0 cm. long. Inflorescences terminal or lateral from few of the uppermost nodes, few- to several-flowered; peduncles 2–4 cm. long, slender; pedicels very slender, 1.0–1.5 cm. long. Flowers small; calyx lobes lanceolate, 2.5–3.0 mm. long; corolla reflexed-rotate, greenish white more or less suffused with purple without, the lobes about 5 mm. long; gynostegium subsessile, white or cream, the column very broadly obconic, about 0.5 mm. long and 1.5 mm. broad, the hoods broadly ovate, about 3 mm. long, the horn strongly adnate, minutely falciform, incurved, shorter than the hoods, the anther head broadly truncate-conic, about 1 mm. long and 2 mm. broad. Follicles unknown.

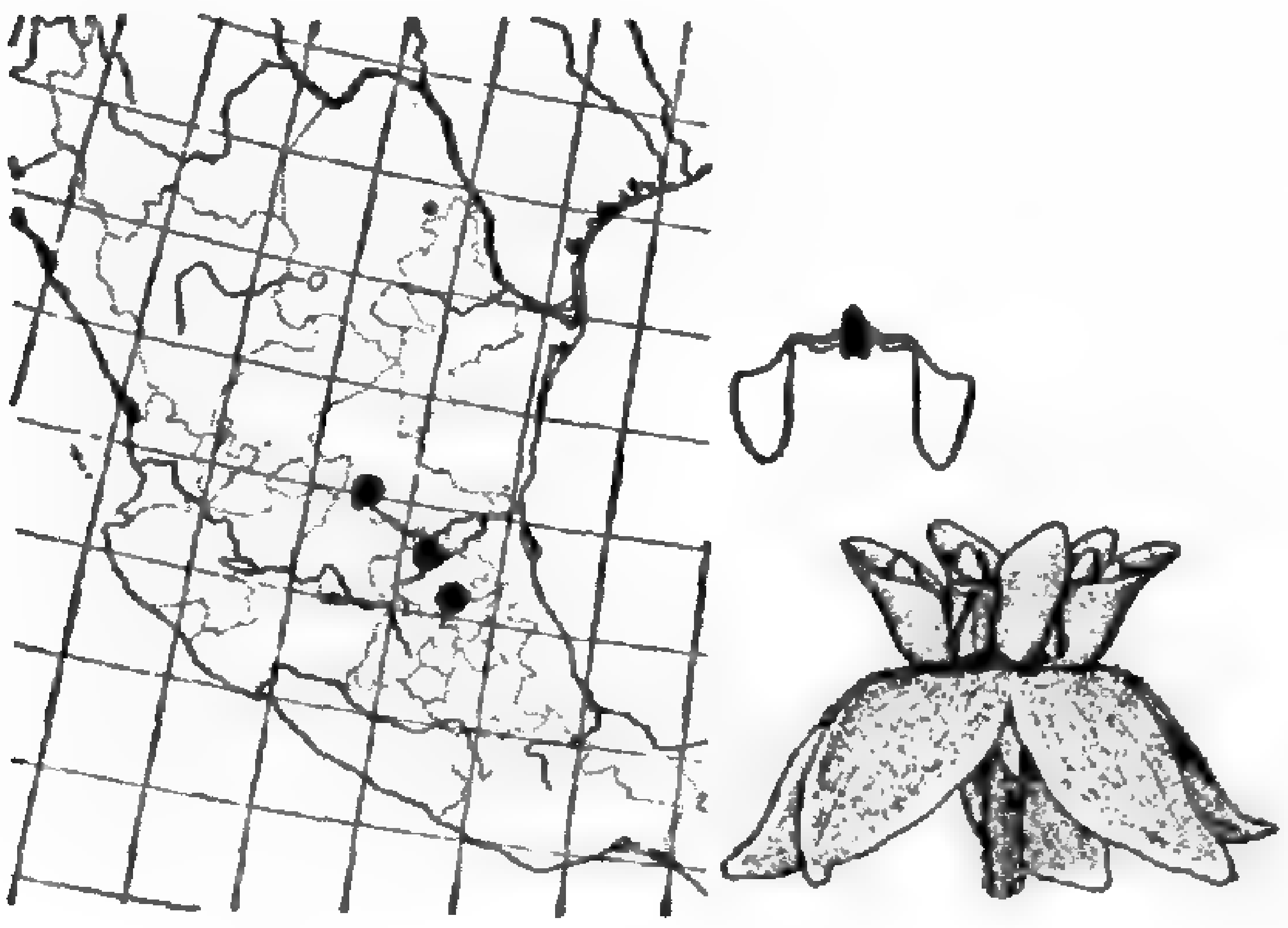

Fig. 61. *Asclepias puberula* A. Gray

In wet or moist places, open meadows in fir forests. Hidalgo and San Luis Potosí. Blooming from June to September.

MEXICO: HIDALGO: Zerezo, Parque Nacional El Chico. SAN LUIS POTOSÍ: Morales.

56. ASCLEPIAS MACROTIS Torr. Bot. Mex. Bound. Surv. 164, *t. 45*. 1859. [T.: *Wright 1691*, MO!]

Suffrutescent perennials. Stems densely clustered from the rootstalk, repeatedly and rather fastigiately branching, very slender and twiggy (rather resembling an Ephedra), 1–3 dm. tall, very inconspicuously puberulent in decurrent lines from the nodes, glabrate at maturity. Leaves opposite, sessile, filiform to acicular, 3.5–8.0 cm. long, 1–4 mm. broad, revolute, glabrous. Inflorescences solitary and lateral from the upper nodes, few- to several-flowered; peduncles slender, 2–10 mm. long; pedicels very slender, about 1 cm. long. Flowers rather small; calyx lobes ovate, 2–3 mm. long; corolla pale greenish yellow, slightly tinged with purple without, the lobes about 5 mm. long; gynostegium subsessile, cream or yellowish, the column about 0.5 mm. long and 2 mm. broad, ovate-lanceolate, the hoods very narrowly acuminate, 4–6 mm. long, the horn strongly adnate, much shorter than the hood, ascending, usually minutely pilosulose at the tip, the anther head truncately conic, about 1 mm. long and 2 mm. broad. Follicles erect on deflexed pedicels, very narrowly fusiform, long-apiculate, 4–7 cm. long, 5–7 mm. thick, smooth, inconspicuously pilosulose to glabrate; seeds oval, about 6 mm. long, white or pale tawny, 2.5–3.5 cm. long.

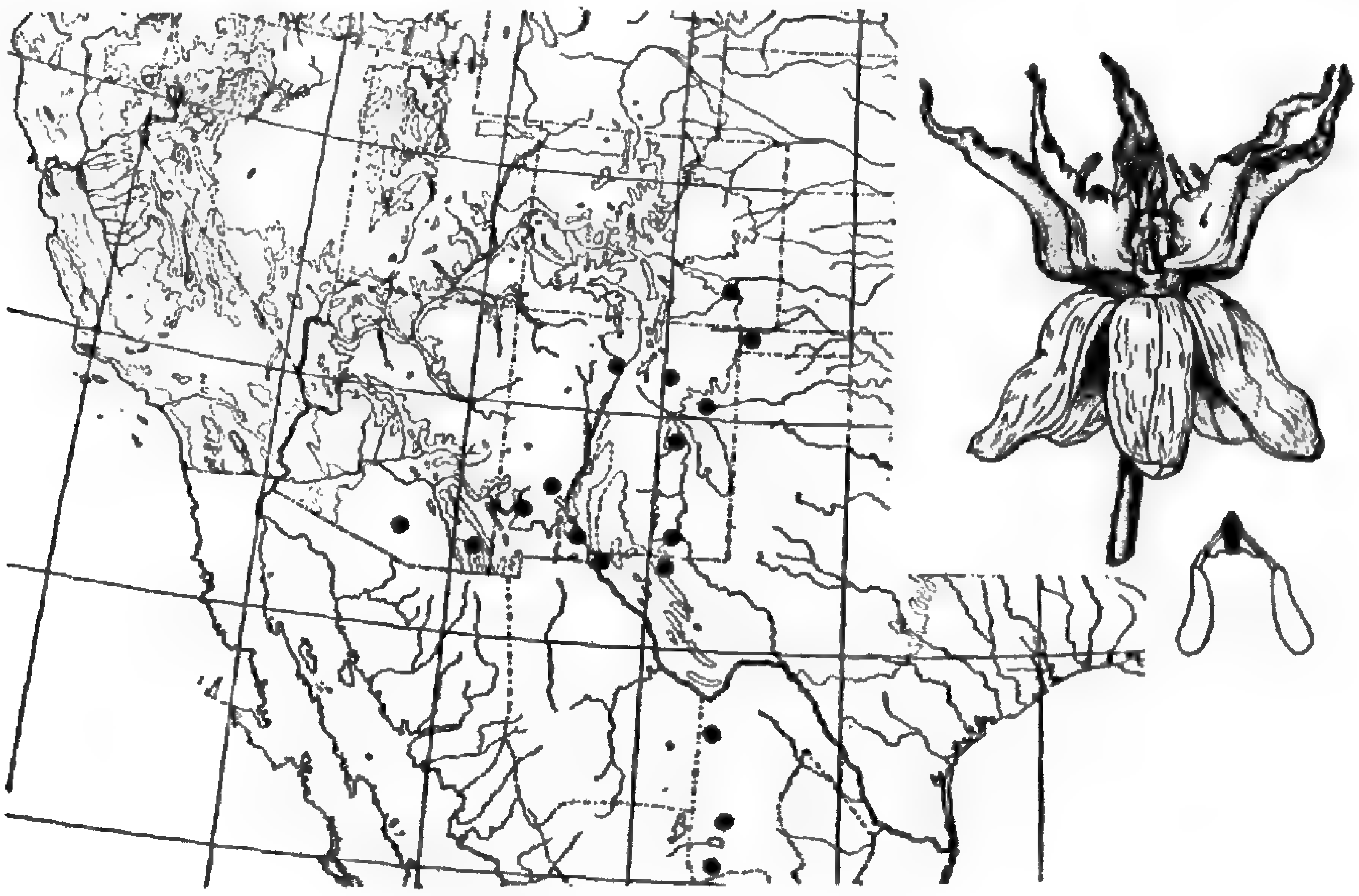

Fig. 62. *Asclepias macrotis* Torr.

Dry hills and mesas. New Mexico and adjacent Colorado, Oklahoma, Texas, and Arizona; northern Coahuila. Blooming from May to October.

United States:
Arizona: Cochise and Pima counties.
Colorado: Otero County.
New Mexico: De Baca, Dona Ana, Eddy, Grant, Quay, San Miguel, Santa Fe, and Sierra counties.
Oklahoma: Cimarron County.
Texas: Culberson and El Paso counties.
Mexico: Coahuila: Múzquiz, G. Cepeda, Picacho de San José, Picacho del Fuste, Sierra de Parras.

An extremely well-marked and constant species, with floral structure quite *sui generis*, particularly the odd horns.

57. Asclepias lemmoni A. Gray, in Proc. Amer. Acad. 19:85. 1883. [T.: *Lemmon s. n.*, MO!]

Asclepias chapalensis Brandg. in Univ. Calif. Publ. Bot. 6:358. 1916. [T.: *Lemmon s. n.*, MO!]

Herbaceous perennials, conspicuously and generally setose-pilose throughout. Stems very stout, simple, 6–8 dm. tall. Leaves opposite, sessile, very broadly and regularly oval, apex broadly rounded, base broadly cordate and amplexicaul, 16–22 cm. long, 9–11 cm. broad, firmly membranaceous. Inflorescences subterminal from few to several of the uppermost nodes, many-flowered; peduncles 6–14 cm. long, rather stout; pedicels more slender, 2–3 cm. long. Flowers large; calyx lobes lanceolate, 5–7 mm. long; corolla pale greenish yellow slightly suffused with purple without, the lobes 1.0–1.3 cm. long; gynostegium shortly stipitate, cream, the column stoutly obconic, about 2 mm. long and 3 mm. broad, the hoods ovate, narrowly acute, widely spreading, 8–9 mm. long, the horn adnate to the base, rather stout and compressed, ascending, much shorter than the hood, the anther head broadly truncate-conic, about 3 mm. long and 4.5 mm. broad. Follicles erect on deflexed pedicels, rather narrowly fusiform and shortly apiculate, 7–12 cm. long, 1.5–2.5 cm. broad, densely setose-pilose; seeds oval, 6–7 mm. long, the pale tawny coma 2–3 cm. long.

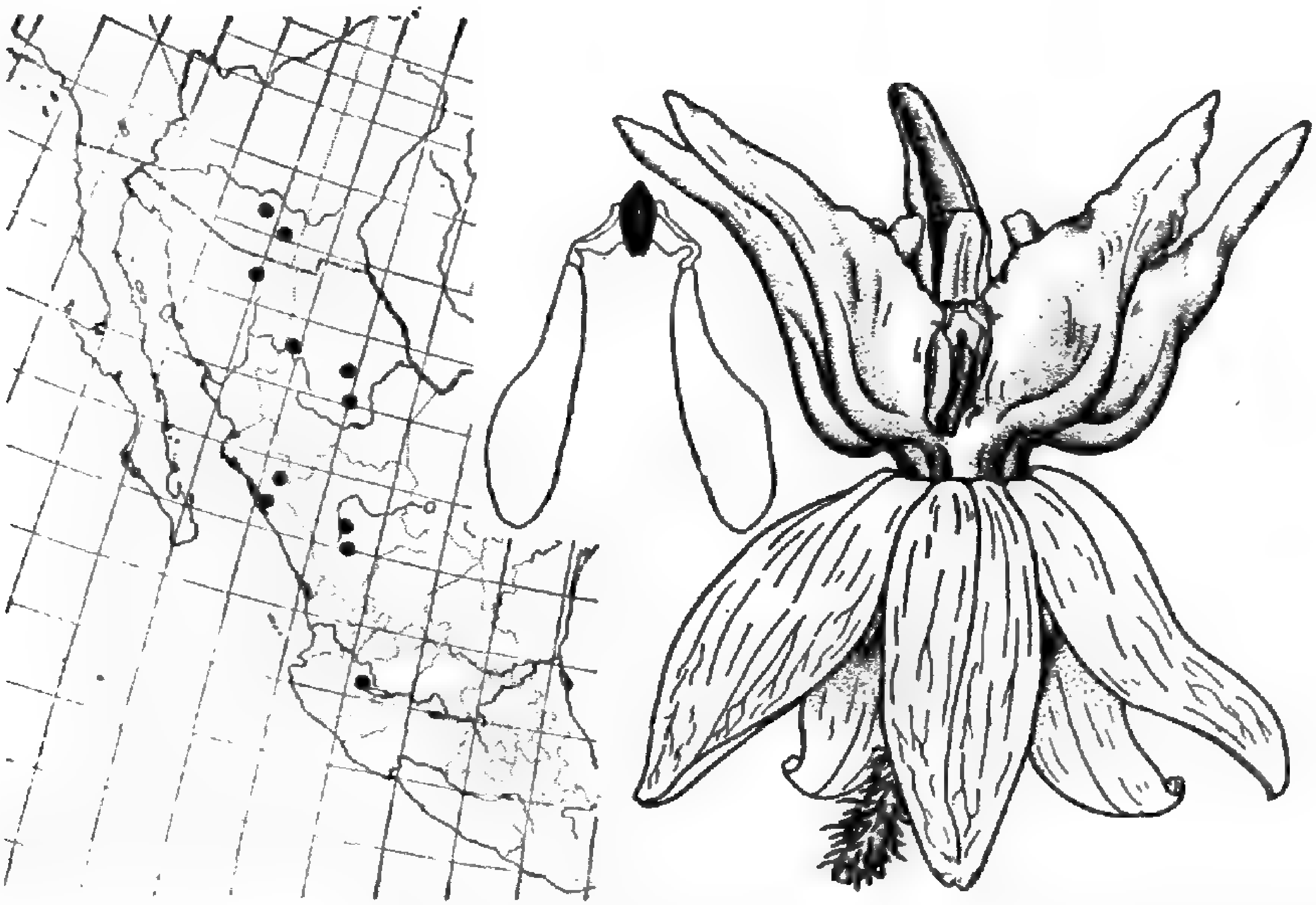

Fig. 63. *Asclepias lemmoni* A. Gray

Rocky limestone slopes and canyons in oak and pine woods. Southern Arizona; Chihuahua to Sonora and southward to Jalisco. Blooming from June to September.

United States:
arizona: Cochise and Pima counties.

Mexico: chihuahua: Temosachic, Majalca, Mapula Mtns. durango: Durango, El Salto. jalisco: Lake Chapala. sinaloa: Culiacán, Cerro Colorado. sonora: San José Mtns.

An unusually distinct and constant species, superficially resembling *A. speciosa*. It is an odd coincidence that Lemmon collected the type specimens of both *A. lemmoni* and *A. chapalensis*, the former in Arizona in 1881 and the latter in Jalisco in 1905.

58. Asclepias laxiflora (Benth.) Dcne. in DC. Prodr. 8:571. 1844.

Otaria laxiflora Benth. Pl. Hartw. 67. 1839. [T.: *Hartweg s. n.*, K!]
Asclepias melantha Dcne. in DC. Prodr. 8:570. 1844. [T.: *Andrieux 233*, P!]

Herbaceous perennials. Stems rather slender, simple, 6–8 dm. tall, minutely puberulent to glabrate in age. Leaves opposite, shortly petiolate, broadly ovate to ovate-lanceolate, apex shortly acute or acuminate, base broadly obtuse to rounded, 6–9 cm. long, 3–4 cm. broad, firmly membranaceous, dark green above, glaucous

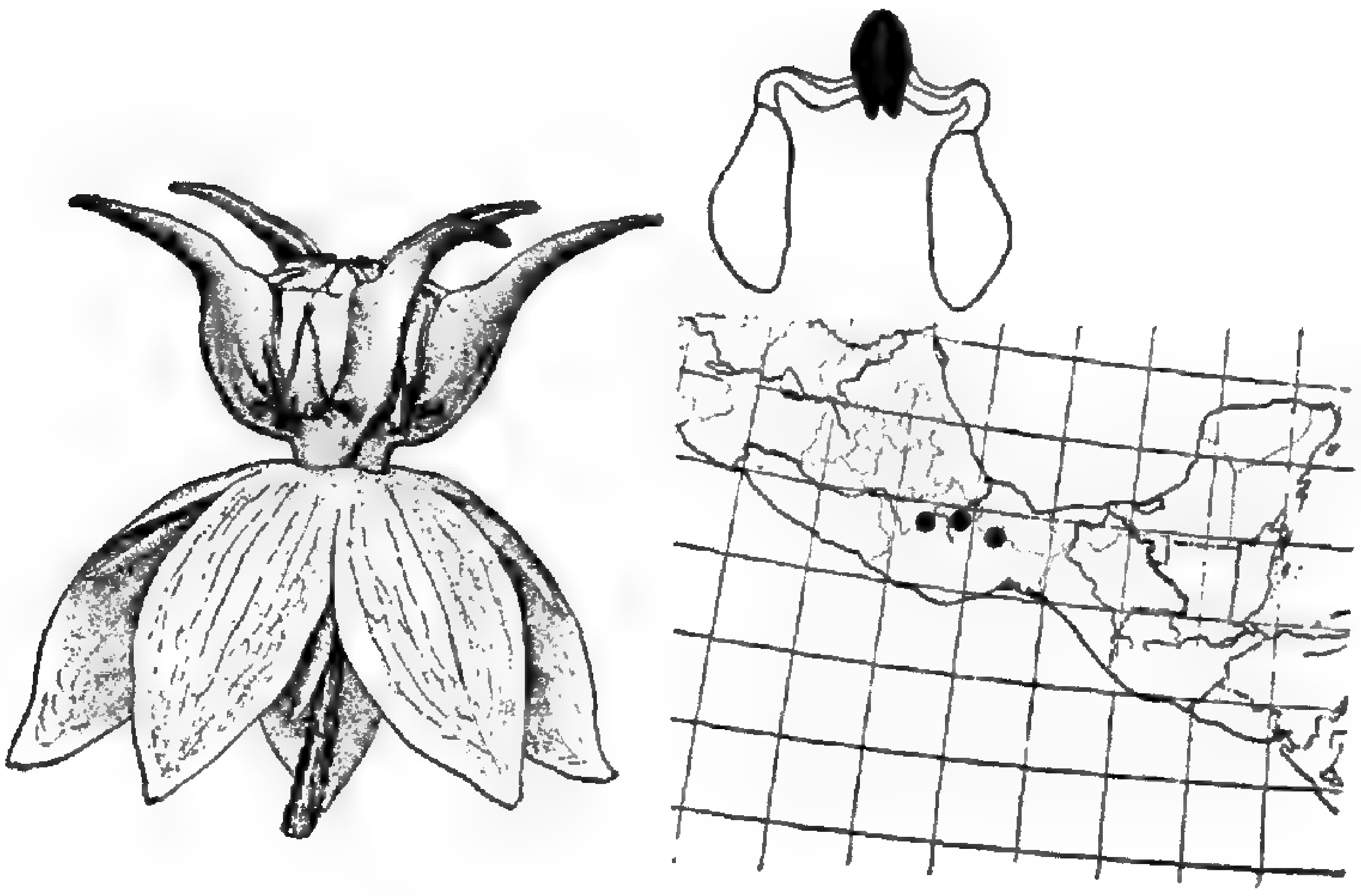

Fig. 64. *Asclepias laxiflora* (Benth.) Dcne.

beneath, inconspicuously puberulent below to glabrate above; petioles 0.5–1.5 cm. long. Inflorescences subterminal from few of the uppermost nodes, few- to several-flowered; peduncles slender, 1–4 cm. long; pedicels slender, about 2 cm. long. Flowers large, showy; calyx lobes ovate-lanceolate, about 4 mm. long, deep purple; corolla reflexed-rotate, deep reddish purple, the lobes 1.0–1.2 cm. long; gynostegium shortly stipitate, deep reddish purple, the column broadly obconic, about 1 mm. long and 2.5 mm. broad, the hoods linear-lanceolate, long-acuminate, spreading, about 8 mm. long, the horn linguiform, about half adnate, incurved, much shorter than the hoods, the anther head truncately conic, about 2.5 mm. long and 3.5 mm. broad. Follicles unknown.

Mountain-sides. Oaxaca. Blooming from May to August.

MEXICO: OAXACA: La Parada, Cerro de Metate, Cerro de San Felipe.

A very showy species superficially resembling *A. hypoleuca* of the north, from which it differs in the nearly glabrous leaves and narrower keeled hoods with very broad marginal lobing and linguiform horns.

Series 8. ROSEAE*

KEY TO THE SPECIES

- a. Stems typically stout and erect; flowers yellowish, rarely somewhat suffused with purple; anther head about three-quarters as long as broad, the wings corneous and acute or spurred at the base.
  - b. Plants herbaceous, the leaves broadly laminate and persistent.
    - c. Inflorescences sessile or subsessile, the peduncles shorter than the subtending petioles or scarcely longer.
      - d. Hoods about as long as the anther head, much shorter than the corolla lobes.
        - e. Leaves variable, relatively small, typically rather oblong and two to three times as long as broad; plants densely puberulent. Coastal Plain: North Carolina to Florida; eastern Texas .... 59. *A. tomentosa*
        - ee. Leaves rather uniform, relatively large, typically almost as broad as long.

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* See also species 31, *Asclepias glaucescens* HBK., and 98, *Asclepias elata* Benth.

f. Leaves subquadrate, definitely petiolate; plants persistently puberulent generally; hoods broadly 2-lobed at the tip, the horn not wholly adnate. South Dakota to Texas and westward to Colorado and New Mexico; northern Chihuahua ....60. *A. arenaria*

ff. Leaves very broadly oval to obovate, subsessile; plants minutely tomentulose when very young, soon becoming glabrate; hoods entire, the horn wholly adnate. Southwestern Nebraska to western Texas and westward to southern Utah and California ....61. *A. latifolia*

dd. Hoods about twice as long as the anther head, about equalling the corolla lobes; plants densely puberulent generally. Coastal Plain: South Carolina to eastern Texas ....62. *A. obovata*

cc. Inflorescences obviously pedunculate, the peduncles much longer than the subtending petioles.

d. Horns about half adnate to the hoods.

e. Plants essentially glabrous; leaves narrowly lanceolate, cuneate, rather irregularly approximate; flowers rather few and lax; follicles pendulous or subpendulous. Eastern Utah ....63. *A. labriformis*

ee. Plants minutely tomentulose when young, soon becoming glabrate; leaves ovate and deeply cordate, minutely erose, opposite; flowers rather many and crowded; follicles erect on deflexed pedicels. Southern California and adjacent Arizona, Nevada, and Utah; Baja California ....64. *A. erosa*

dd. Horns wholly adnate to the hoods; plants densely and persistently puberulent or tomentulose, cordate, entire, opposite or irregularly approximate; flowers rather many and crowded; follicles erect on deflexed pedicels. California; Baja California ....65. *A. eriocarpa*

bb. Plants fruticose or suffruticose, the leaves filiform, caducous.

c. Hoods about equalling the anther head, scarcely saccate at the base.

d. Hoods erect, the horn conspicuously exserted and arching over the anther head, without a posterior crest. Southwestern Baja California........66. *A. masonii*

dd. Hoods spreading, the horn barely exserted and abruptly inflexed toward the anther head, with a broad posterior crest. Coastal Sinaloa ....67. *A. subaphylla*

cc. Hoods appearing much shorter than the anther head, conspicuously saccate at the base. Extreme southern California and adjacent Arizona; Baja California......68. *A. albicans*

aa. Stems typically rather slender, frequently subscapose, clustered from the base and more or less decumbent; flowers red to pinkish, rarely white; anther head about half as long as broad, the wings pergamentaceous and broadly rounded at the base.

b. Plants relatively stout, more or less densely arachnoid-tomentose to glabrate generally, the stems 2–7 dm. long; inflorescences sessile or subsessile even when términal. Southern to central California ....69. *A. vestita*

bb. Plants relatively slender and frequently subscapose, cinereous-tomentulose to glabrate generally, the stems usually 4–15 cm. long; inflorescences long-pedunculate.

c. Leaves broadly ovate to suborbicular; follicles broadly fusiform. Southwestern Texas and southern New Mexico and Arizona; Chihuahua to Sonora and southward to Durango and San Luis Potosí ....70. *A. nummularia*

cc. Leaves linear to filiform; follicles narrowly fusiform. Jalisco to Chiapas; Guatemala ....71. *A. rosea*

This series quite possibly is polyphyletic, representing more or less parallel extremes derived from SYRIACAE, PURPURASCENTES, and MACROTIDES. The tendency toward saccate hoods and complete fusion of the horn may show transition to the subgenus SOLANOA; in fact *A. albicans* might almost as well be referred there.

59. ASCLEPIAS TOMENTOSA Ell. Sketch Bot. S. Car. & Ga. 1:320. 1821, ex char.

Asclepias megalotis Raf. New Fl. North Amer. 4:61. 1838, ex char.
Asclepias aceratoides M. A. Curtis, in Amer. Jour. Sci. Ser. II, 7:407. 1849, ex char.

Herbaceous perennials. Stems rather stout, simple or branching rather infrequently, 2–7 dm. tall, softly and rather inconspicuously appressed-puberulent. Leaves opposite, petiolate, variable in outline and size, typically rather oblong or oval to oblong-lanceolate or obovate, apex usually obtuse, to acute or rounded and

Fig. 65. *Asclepias tomentosa* Ell.

somewhat retuse, base broadly acute to rounded, 4–9 cm. long, 1.5–5.0 cm. broad, firmly membranaceous, dark green above, pale beneath, softly and generally puberulent particularly below; petioles about 1 cm. long. Inflorescences lateral and solitary at several or numerous of the upper nodes, sessile or subsessile, several- to many-flowered; pedicels 1.5–2.0 cm. long, softly puberulent. Flowers rather large; calyx lobes lanceolate, 3–6 mm. long; corolla pale yellowish green somewhat flushed with orange without, the lobes 9–10 mm. long; gynostegium yellowish cream, very shortly stipitate, the column obconic, about 1.5 mm. long and 3 mm. broad, the hoods obovate-subquadrate, truncate, about 4 mm. long, the horn wholly adnate, falciform, sharply incurved, longer than the hood, the anther head truncately conic, about 3.5–4.0 mm. long and 5–6 mm. broad. Follicles erect on deflexed pedicels, narrowly fusiform, 10–12 cm. long, about 1 cm. broad, smooth, softly puberulent to glabrate; seeds broadly oval, about 1 cm. long, the pale tawny coma about 4.5 cm. long.

Sandy soil; pine barrens. North Carolina to Florida; eastern Texas. Blooming from May to June.

United States:

FLORIDA: Brevard, Collier, De Soto, Duval, Lake, Marion, Orange, Osceola, Putnam, and Volusia counties.

NORTH CAROLINA: Harnett County.

SOUTH CAROLINA: Darlington County.

TEXAS: Polk County.

This is the only species east of the Mississippi River with the very strongly adnate horns so typical of numerous western and Mexican species. Because of its very limited distribution in Florida and the adjacent coastal plain, I am inclined to view it as a relatively ancient species and consequently this particular type of hood as having been evolved rather early.

60. **Asclepias arenaria** Torr. in Bot. Mex. Bound. Surv. 162. 1859. [T.: *Wislizenus s. n.*, MO!]

Herbaceous perennials. Stems relatively stout, simple or branching infrequently, densely tomentulose. Leaves opposite, petiolate, very broadly obovate-oval and more or less subquadrate, apex broadly rounded and more or less retuse, base truncate or broadly rounded and occasionally somewhat cordate, rather uniform in shape and size, 6–9 cm. long, 4–8 cm. broad, firmly membranaceous, concolorous, more or less generally white-tomentulose particularly beneath; petioles 0.5–1.3 cm. long. Inflorescences lateral and solitary at several to many of the upper nodes, rather many-flowered; peduncles obsolete to about 2 cm. long, densely tomentulose; pedicels rather stout, 1–2 cm. long, densely white-tomentulose. Flowers rather large; calyx lobes ovate-lanceolate, 6–7 mm. long, densely and minutely white-tomentulose; corolla reflexed-rotate, pale green, the lobes 9–10 mm. long; gynostegium shortly stipitate, white or cream, the column obconic, about 2 mm. long and 3.5 mm. broad, the hoods more or less broadly 2-lobed at the tip, subquadrate,

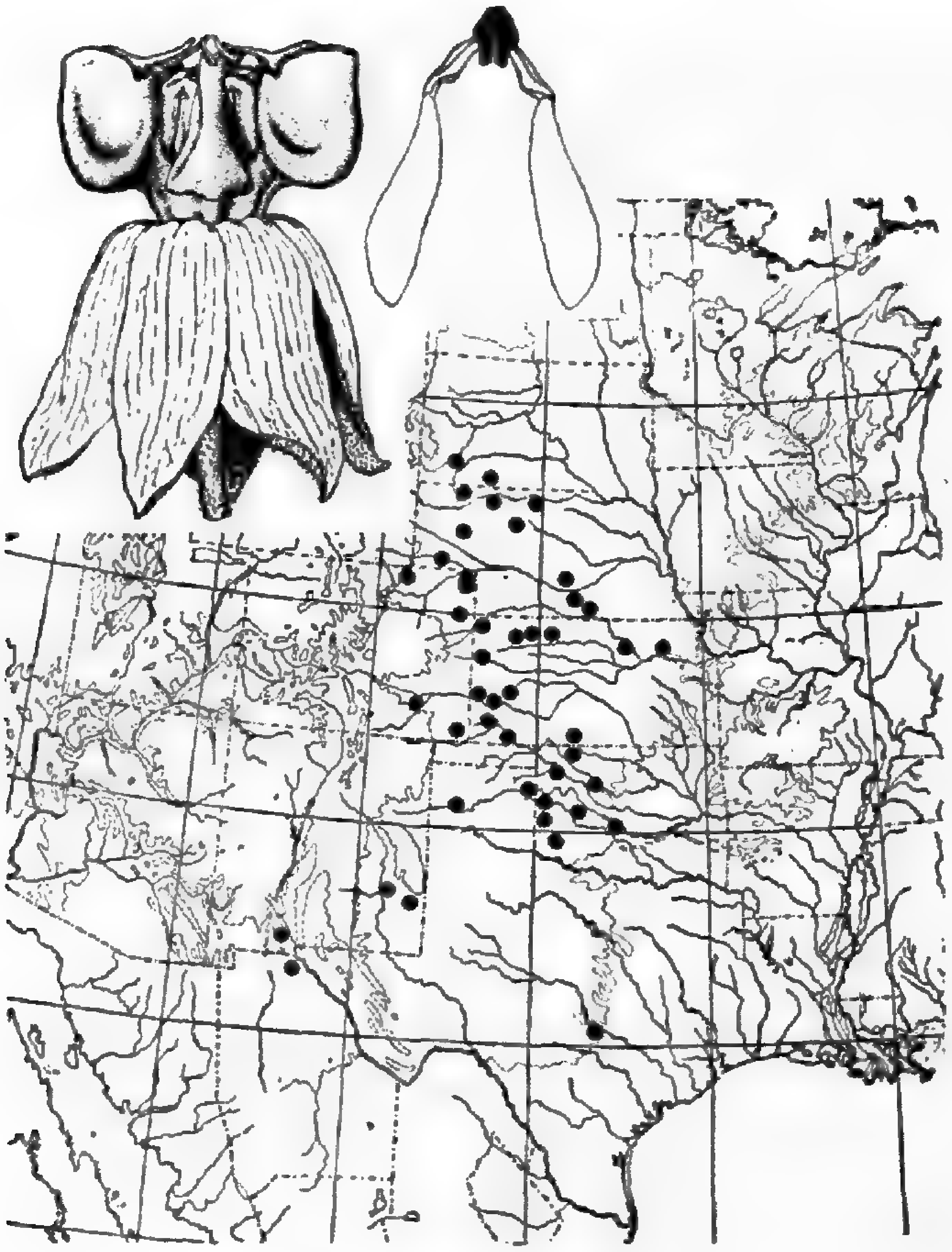

Fig. 66. *Asclepias arenaria* Torr.

the horn about half adnate, rather narrowly falciform, sharply incurved, somewhat longer than the hood, the anther head truncately conic, about 3 mm. long and 4 mm. broad. Follicles erect on deflexed pedicels, rather broadly fusiform and shortly apiculate, 7–9 cm. long, 1.5–2.5 cm. broad, finely tomentulose to glabrate; seeds broadly oval, about 11 mm. long, the pale tawny coma about 2.5 cm. long.

Sandy soil, spreading to roadsides. South Dakota to Texas and westward to Colorado and New Mexico; Chihuahua. Blooming from May to August.

UNITED STATES:

COLORADO: Baca, Otero, Phillips, Sedgwick, Weld, and Yuma counties.

KANSAS: Barber, Cheyenne, Finney, Graham, Grant, Hamilton, Kearney, Riley, Rooks, Seward, Shawnee, Sheridan, and Wallace counties.

NEBRASKA: Brown, Buffalo, Cherry, Cheyenne, Franklin, Garden, Kearney, Sheridan, and Thomas counties.

NEW MEXICO: Chaves, Dona Ana, and Roosevelt counties.

OKLAHOMA: Beckham, Cleveland, Grady, Greer, Kingfisher, Roger Mills, Woodward, and Woods counties.

SOUTH DAKOTA: Bennett and Washington counties.

TEXAS: Bastrop, Hemphill, and Potter counties.

MEXICO: CHIHUAHUA: Paso del Norte, Samalayuca.

The characteristic broad 4 lobes of the corona hoods apparently consist of two marginal auricles, with the median lobe broadly retuse, as in the leaves.

Torrey does not cite a collector of the type specimen, but in the herbarium of the Missouri Botanical Garden is an excellent specimen collected on the Jornado del Muerte in 1846 by Wislizenus on his perilous and eventful buggy trip into the midst of the Mexican war. I feel that this probably represents the type of the species.

61. ASCLEPIAS LATIFOLIA Raf. Atl. Jour. 146. 1832. [Based on *Asclepias obtusifolia β latifolia* Torr.]

Asclepias obtusifolia β ? latifolia Torr. in Ann. Lyc. Nat. Hist. N. Y. 2:217. 1828.
Otanema latifolia (Raf.) Raf. New Fl. North Amer. 4:61. 1838.
Asclepias jamesii Torr. Bot. Mex. Bound. Surv. 162. 1859. [Based on *Asclepias obtusifolia β? latifolia* Torr.]

Herbaceous perennials. Stems stout, simple or infrequently branching, 2–6 dm. tall, minutely tomentulose when very young, soon becoming glabrate. Leaves opposite, very shortly petiolate, very broadly oval-obovate, apex broadly rounded and frequently somewhat retuse, base very broadly rounded and frequently somewhat cordate, 4–16 cm. long, 4–13 cm. broad, firmly membranaceous and somewhat coriaceous, concolorous and somewhat glaucous, minutely white-tomentulose generally when very young, soon glabrate; petioles about 5 mm. long. Inflorescences lateral at several to numerous of the upper nodes, subsessile or very shortly pedunculate, many-flowered; peduncles obsolete to 1.5 cm. long; pedicels rather slender, 2.5–3.0 cm. long, minutely white-tomentulose. Flowers rather large; calyx lobes ovate-lanceolate, about 4 mm. long; corolla reflexed-rotate, pale green sometimes tinted purplish without, the lobes 11–12 mm. long; gynostegium shortly stipitate, greenish white, the column broadly obconic, about 2 mm. long and 3 mm. broad, the hoods subquadrate, truncate or broadly retuse, about 4 mm. long, the horn wholly adnate, very broadly falciform, sharply incurved, somewhat longer than the hood, the anther head about 3 mm. long and 4 mm. broad, truncately conic. Follicles erect on deflexed pedicels, broadly fusiform, shortly apiculate, 6–8 cm. long, 1.5–3.0 cm. broad, smooth, essentially glabrous; seeds oval, about 7 mm. long, the pale tawny coma about 2 cm. long.

Mixed prairies, badlands, and high plains, spreading to roadsides and railways. Southwestern Nebraska and western Texas westward to southern Utah and southeastern California. Blooming from May to September.

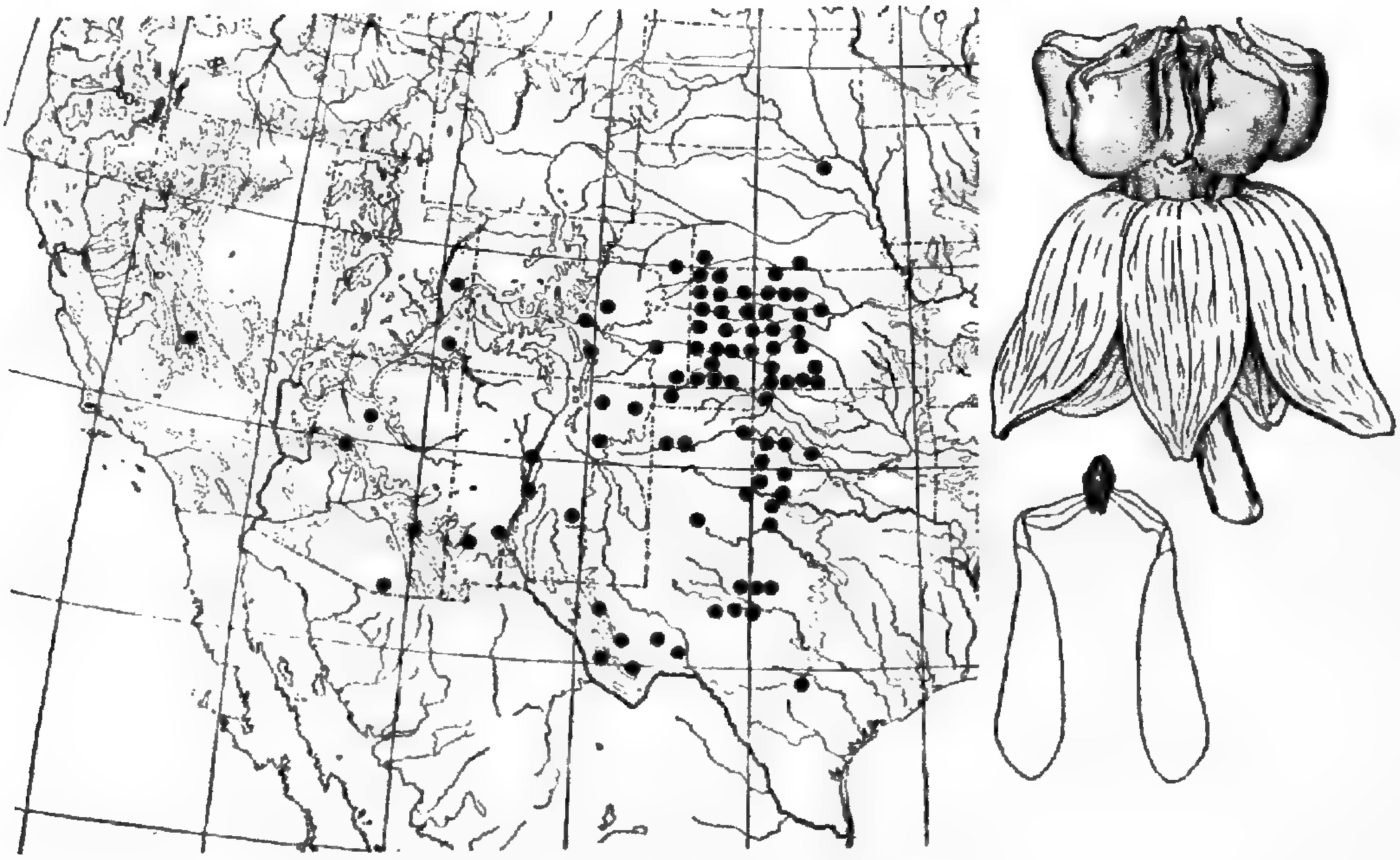

Fig. 67. *Asclepias latifolia* Raf.

United States:

ARIZONA: Coconino, Graham, Santa Cruz, and Yavapai counties.

CALIFORNIA: Inyo County.

COLORADO: Baca, Bent, El Paso, Fremont, Huerfano, and Yuma counties.

KANSAS: Barber, Barton, Cheyenne, Clark, Comanche, Ellis, Finney, Gove, Graham, Grant, Greely, Hamilton, Harper, Haskell, Hodgeman, Kearney, Kingman, Kiowa, Lane, Lincoln, Logan, Meade, Morton, Ness, Osborne, Pawnee, Phillips, Rawlins, Rooks, Rush, Russell, Scott, Seward, Selkirk, Sheridan, Sherman, Stafford, Stanton, Stevens, Thomas, Trego, Wallace, and Wichita counties.

NEBRASKA: Dundy, Franklin, and Knox counties.

NEW MEXICO: Bernalillo, Colfax, Grant, Lincoln, San Miguel, Sierra, Socorro, and Union counties.

OKLAHOMA: Beckham, Canadian, Cimarron, Custer, Harmon, Harper, Kiowa, Roger Mills, and Tillman counties.

TEXAS: Baylor, Bexar, Brewster, Callahan, Childress, Concho, Culberson, Hemphill, Irion, Jeff Davis, Lubbock, Nolan, Oldham, Pecos, Presidio, Terrell, Tom Green, and Willbarger counties.

UTAH: Grand and San Juan counties.

Somewhat resembling *A. arenaria* except for its glabrity, but with very different hoods. I have seen no intergrading specimens. Both species are extremely distinct and uniform.

62. **Asclepias obovata** Ell. Sketch Bot. S. Car. & Ga. 321. 1821, ex char. [T.: *Jackson s. n.*]

Asclepias viridiflora γ *obovata* (Ell.) Torr. Fl. North & Mid. U. S. 1:284. 1824.
Acerates obovata (Ell.) Eaton, Man. ed. 6, 3. 1833.
Polyotus obovatus (Ell.) Nutt. in Trans. Amer. Phil. Soc. N. S. 5:201. 1837.

Herbaceous perennials from a rather deep slender rootstalk. Stems rather stout, simple or branching infrequently, 1.5–5.0 dm. tall, softly tomentulose. Leaves opposite, shortly petiolate, quite variable in size and outline, the lowermost usually broadly oval or oblong, becoming narrower and smaller above, apex broadly acute to rounded, base obtuse to rounded or truncate, 3–8 cm. long, 1–3 cm. broad, firmly membranaceous, densely tomentulose particularly beneath; petioles 0.5–1.0 cm. long. Inflorescences terminal, solitary or also lateral from the uppermost few nodes, several- to rather many-flowered, subsessile to very shortly pedunculate, densely tomentulose; peduncles obsolete to about 5 mm. long; pedicels rather stout, 8–10 mm. long. Flowers rather large; calyx lobes ovate-lanceolate, 4–5 mm. long, pilosulose; corolla reflexed-rotate, pale greenish yellow, the lobes 9–10 mm. long;

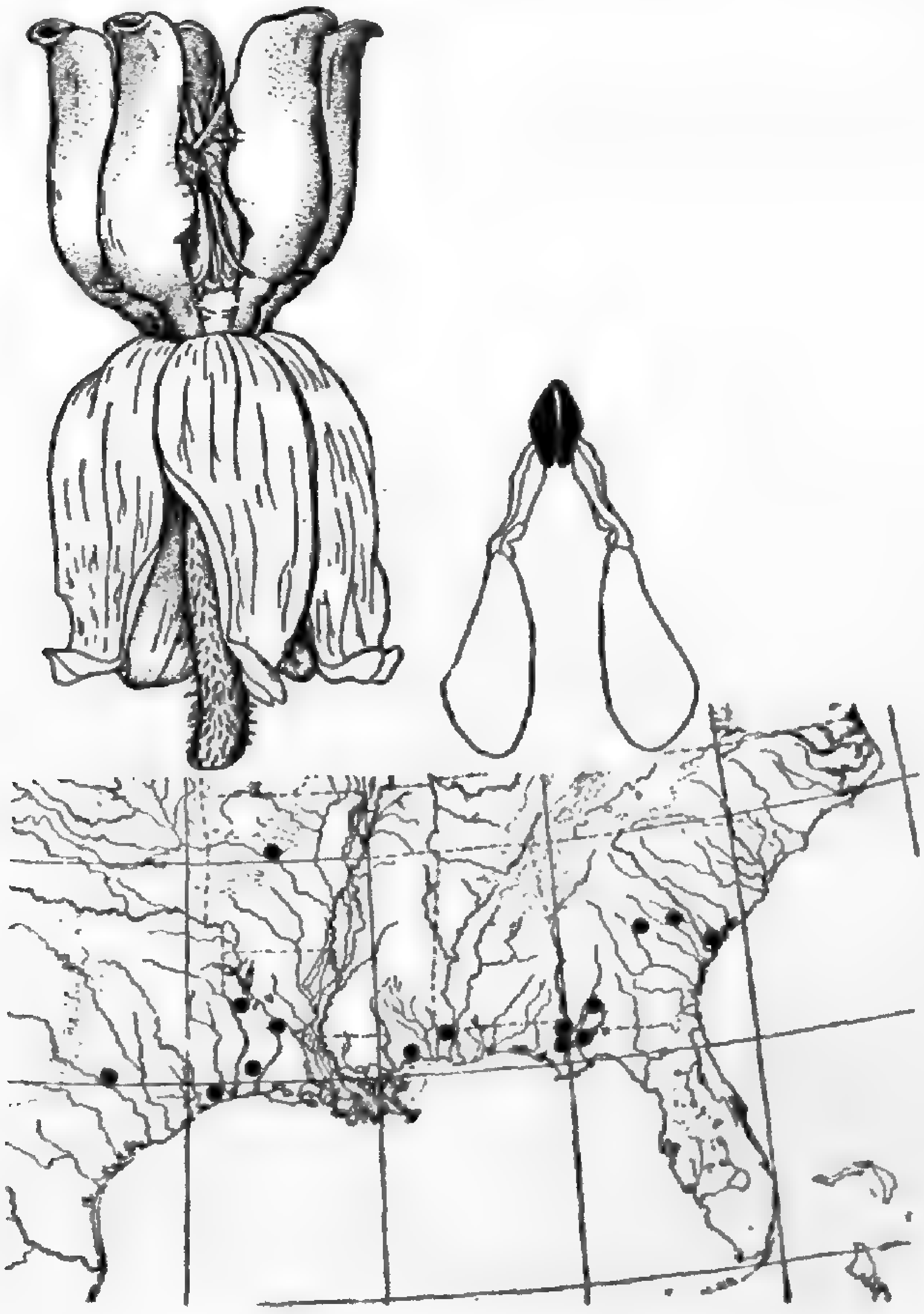

Fig. 68. *Asclepias obovata* Ell.

gynostegium shortly stipitate, pale greenish orange, the column obconic, about 1.5 mm. long and 2 mm. broad, the hoods broadly oblong-oval, rounded, about 6 mm. long, the horn basally adnate, rather narrowly falciform, sharply incurved, about as long as the hoods, the anther head truncately conic, about 3 mm. long and 4 mm. broad. Follicles erect on deflexed pedicels, tomentose when young, unknown when mature.

Sandy oak and pine woods, spreading to fields and roadsides. South Carolina to Florida and westward to eastern Texas. Blooming from June to August.

United States:
alabama: Mobile County.
florida: Calhoun, Gadsden, and Jackson counties.
georgia: Jenkins, Laurens, and Mitchell counties.
louisiana: Calcasieu, Natchitoches, and Rapides parishes.
mississippi: Harrison County.
south carolina: Beaufort County.
texas: Austin, Bastrop, Houston, Jefferson, Leon, and Polk counties.

It is unfortunate that Elliott's type is not still preserved at the Charleston Museum. Elliott compares his species to *A. viridiflora* and states that his specimen had been so injured that he could not determine the presence or absence of a horn. Taking this cue, some botanists have considered *A. obovata* to be merely the broad-leaved phase of *A. viridiflora* or at best a related species. Elliott's description of the "leaves of the crown twice as long as the corpuscle [i.e. anther head]" at once removes that possibility and assures the present, and traditional, interpretation.

The species is a very odd one, somewhat reminiscent of *A. meadii,* but definitely seems more naturally related to *A. tomentosa,* although with much longer hoods.

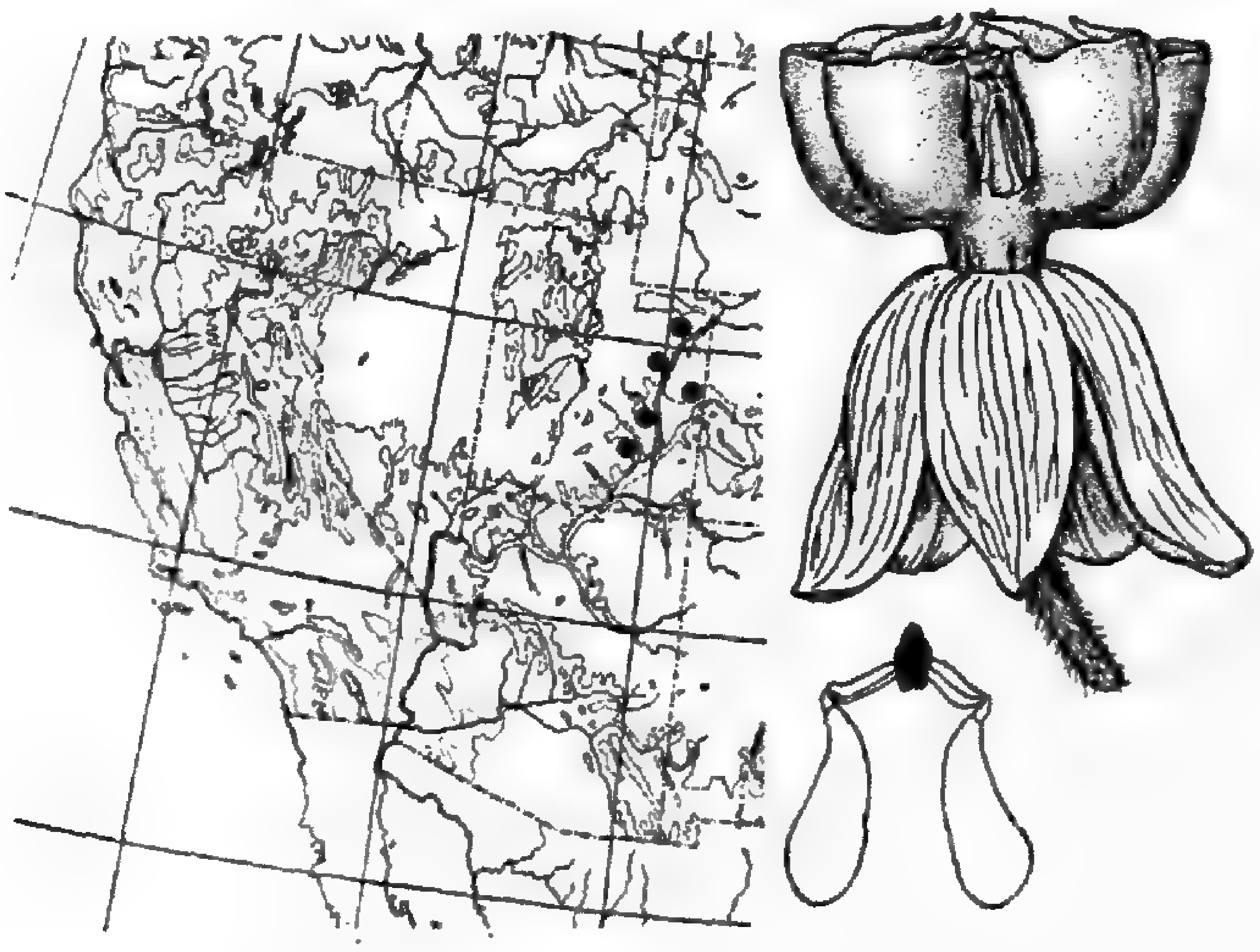

Fig. 69. *Asclepias labriformis* M. E. Jones

63. Asclepias labriformis M. E. Jones, in Proc. Calif. Acad. Ser. II, 5:708. 1895. [T.: *M. E. Jones 5650,* MO!]

Herbaceous perennials. Stems rather slender, simple or branching infrequently, 2–5 dm. tall, very inconspicuously puberulent when very young, soon becoming glabrate. Leaves irregularly approximate, subsessile, lanceolate to linear-lanceolate above, apex acute to acuminate, base acutely cuneate, 5–15 cm. long, 0.6–2.5 cm. broad, firmly membranaceous or somewhat subsucculent, pale green, essentially glabrous. Inflorescences lateral and solitary at several of the upper nodes, definitely pedunculate, few- to several-flowered; peduncles somewhat stout, 0.4–3.0 cm. long; pedicels slender, 1.5–2.0 cm. long. Flowers mediocre; calyx lobes lanceolate, 4–5 mm. long; corolla pale yellowish green, the lobes about 8 mm. long; gynostegium shortly stipitate, cream, the column rather narrowly cylindrical, about 1.5 mm. long and 2 mm. broad, the hoods subquadrate, truncate, about 3–4 mm. long, the horn about half adnate, rather narrowly falciform, incurved, somewhat longer than the hood, the anther head truncately conic, about 1.5 mm. long and 2 mm. broad. Follicles on deflexed or pendulous peduncles, ovoid to very broadly fusiform, very shortly apiculate, 4–7 cm. long, 1.5–3.0 cm. broad, smooth, glabrous; seeds very broadly oval, 1–2 cm. long, the pale tawny coma 1.5–1.7 cm. long.

Washes, sandstone canyons, dry cliffs, and high flats. Eastern Utah. Blooming from May to August.

UNITED STATES:
UTAH: Carbon, Emery, Grand, Uintah, and Wayne counties.

Although very easily recognized, *A. labriformis* is rather difficult to place with natural affinities. I am placing it in series ROSEAE even though the horns are not strongly adnate and the column is a bit too narrow.

64. ASCLEPIAS EROSA Torr. Bot. Mex. Bound. Surv. 162. 1859. [T.: *Thurber s. n.*, US!]

Asclepias leucophylla Engelm. in Parry, in Amer. Nat. 9:348. 1875. [T.: *Parry 207*, MO!]
Asclepias demissa Greene, Leafl. Bot. Obs. & Crit. 2:231. 1912. [T.: *Loew s. n.*, US!]
Asclepias obtusata Greene, loc. cit. 232. 1912. [T.: *Rothrock s. n.*, US!]
Asclepias rothrockii Greene, loc. cit. 1912. [T.: *Rothrock s. n.*, US!]

Massive herbaceous perennials, more or less woody at the base. Stems very stout, simple or branching infrequently, 1–2 m. tall, minutely tomentulose when young, soon glabrate. Leaves opposite, sessile, broadly ovate, occasionally broadly oblong-elliptic, apex rather shortly acuminate, base broadly cordate and amplexicaul or the uppermost rounded or subtruncate, 6–24 cm. long, 2.5–11.0 cm. broad, firmly membranaceous or somewhat subcoriaceous or subsucculent, the margins minutely erose, conspicuously white arachnoid-tomentulose when young, becoming glabrate, pale green. Inflorescences solitary or rarely paired at few to several of the uppermost nodes, usually very many-flowered, definitely pedunculate; peduncles 2–12 cm. long, white-tomentulose; pedicels rather slender, 1.2–3.5 cm. long, very densely white-tomentulose. Flowers rather large; calyx lobes lanceolate, 4–6 mm. long, densely white-tomentulose; corolla pale yellowish green, the lobes 9–10 mm. long; gynostegium shortly stipitate, greenish white or cream, the column obconic, about 2 mm. long and 3 mm. broad, the hoods very broadly oval, broadly obtuse at the tip, about 4 mm. long, the horn rather strongly adnate, falciform, incurved, about

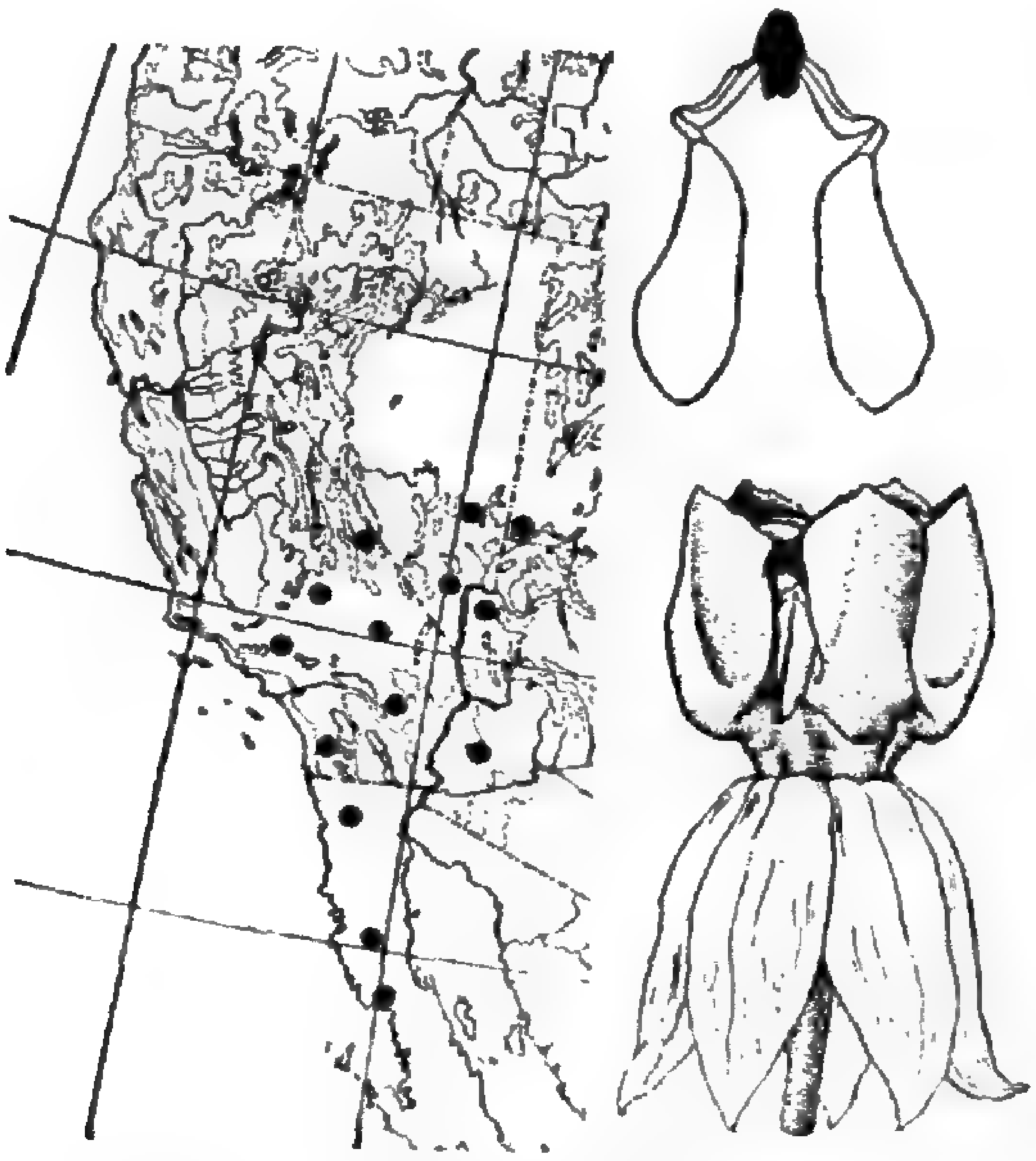

Fig. 70. *Asclepias erosa* Torr.

as long as the hood, the anther head truncately conic, about 3 mm. long and 4 mm. broad. Follicles erect on deflexed pedicels, broadly fusiform, rather shortly apiculate, 5–7 cm. long, 2–3 cm. broad, smooth, glabrous; seeds very broadly oval, about 1.3 cm. long, the pale tawny coma about 1.5 cm. long.

Gulches, washes, and canyons, Mohave and Colorado deserts. Southern California and adjacent Utah, Nevada, and Arizona; Baja California. Blooming from April to October.

UNITED STATES:
ARIZONA: Mohave and Yuma counties.
CALIFORNIA: Inyo, Kern, Los Angeles, Riverside, San Bernardino, and San Diego counties.
NEVADA: Clark and Lincoln counties.
UTAH: Washington County.
MEXICO: BAJA CALIFORNIA: Mission de San Pedro, Vallejo Mtns., Agua Dulce, San Felipe.

One of the largest American milkweeds, the habit somewhat recalling *Calotropis procera* of the Old World.

65. ASCLEPIAS ERIOCARPA Benth. Pl. Hartw. 323. 1849. [T.: *Hartweg 127*, K!]

Asclepias fremontii Torr. Rept. Pacif. R. R. Surv. 6:87. 1857. [T.: *Bigelow s. n.*, US!]
Asclepias kotolo Eastw. in Zoe 5:86. 1900. [T.: *Hudson s. n.*, CAS!]
Asclepias eriocarpa var. *microcarpa* Munz & Johnston, in Bull. Torrey Bot. Club 49:355. 1923. [T.: *Johnston 2833*, CAS!]

Herbaceous perennials. Stems rather stout, simple or branching infrequently, 4–10 dm. tall, densely white-tomentulose above, becoming glabrate below. Leaves opposite to irregularly approximate, shortly petiolate, oblong to oval, apex shortly acuminate to obtuse, base obtuse to rounded or subtruncate, frequently shallowly cordate, 8–20 cm. long, 3–8 cm. broad, firmly membranaceous, white-tomentulose particularly above, at length becoming glabrate; petioles 0.5–1.0 cm. long. Inflorescences lateral from few to several of the uppermost nodes, obviously pedunculate; peduncles 1–10 cm. long, rather stout, white-tomentulose; pedicels slender, 2–5 cm. long, very densely white-tomentulose. Flowers moderately large; calyx lobes ovate-lanceolate, 4–5 mm. long, minutely tomentulose; corolla reflexed-rotate, greenish or yellowish cream sometimes flushed with rose without, the lobes 7–9 mm. long; gynostegium shortly stipitate, cream frequently tinged with rose, the column about 1 mm. long and 2 mm. broad, the hoods very broadly oval, 3–4 mm. long, the horn wholly adnate, very broadly falciform, sharply incurved, somewhat longer than the hood, the anther head truncately conic, about 3 mm. long and 4 mm. broad. Follicles erect on deflexed pedicels, broadly fusiform, shortly apiculate, 5–9 cm. long, 2–3 cm. broad, smooth, densely white-tomentose; seeds broadly oval, 8–9 mm. long, the tawny coma 1.5–3.0 cm. long.

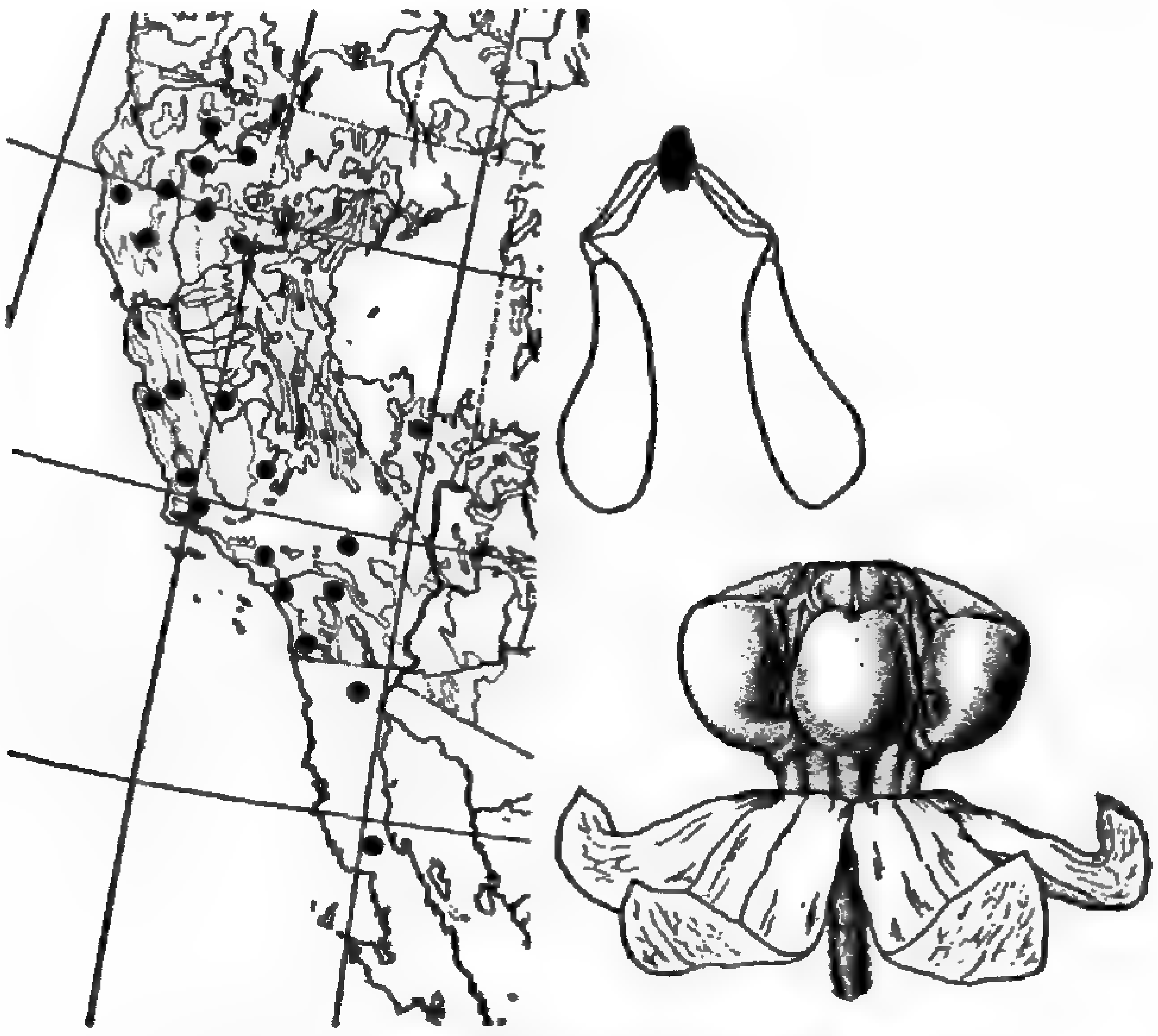

Fig. 71. *Asclepias eriocarpa* Benth.

Adobe flats, rocky barrens, open woods, fields, stream banks, spreading to roadsides. California; Baja California. Blooming from May to October.

United States:

california: Butte, Fresno, Glenn, Kern, Lake, Lassen, Los Angeles, Mendocino, Monterey, Nevada, Orange, Riverside, San Benito, San Bernardino, San Diego, San Luis Obispo, Santa Barbara, Shasta, and Tehama counties.

Mexico: baja california: Sierra San Pedro Martir, Sierra Juarez.

The leaves of *A. eriocarpa* are predominantly opposite, but the nodes are frequently more or less displaced and whorls of three or four are occasional.

66. Asclepias **masonii** Woodson, spec. nov.

Suffrutices subaphylli glaucescentes altitudine ignoti. Caules graciles albescentes glabri aliquando compositi post aetatem florentem aphylli. Folia opposita sessilia linearia vel filiformia ca. 2–5 cm. longa ca. 1 mm. lata mox caduca. Inflorescentiae e nodis superioribus laterales breviuscule pedunculatae pluriflorae; pedunculis 1–3 cm. longis minute pilosulis; pedicellis gracillimis ca. 1.5 cm. longis pilosulis. Flores majusculi; calycis laciniis ovato-lanceolatis ca. 3 mm. longis minute puberulis;

corolla dilute gilva, lobis 7–8 mm. longis; gynostegio breviter stipitato lacteo, columna obconica ca. 1.5 mm. longa 2.5 mm. lata, cucullis erectis ovalibus 7–8 mm. longis, cornu valde adnato simplice et late falciformi valde exserto cucullum superante, androecio truncate conico ca. 2.5 mm. longo et 4.5 mm. lato. Folliculi in pedunculo pendulo anguste fusiformes anguste apiculati 10–13 cm. longi ca. 1.5 cm. lati inermes juventate minute pilosuli mox glabri; seminibus ovalibus ca. 5 mm. longis, coma pallide fulva ca. 2.5 mm. longa.—Holotypus: *J. N. Rose 16305* in Herb. U. S. Nat. Mus. (Santa Margarita Isl., Baja California, Mexico, March 20, 1911).

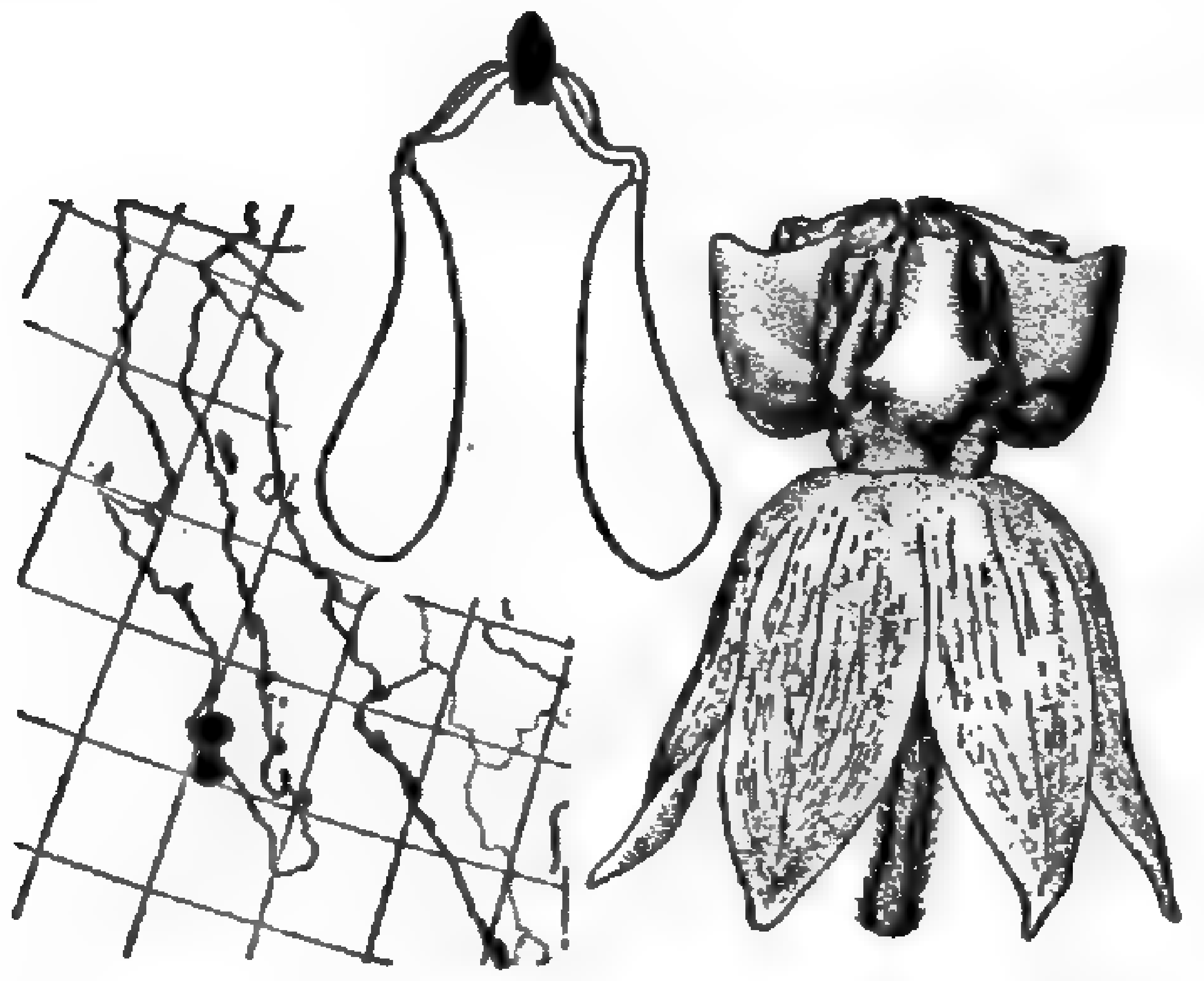
Fig. 72. *Asclepias masonii* Woods.

I am naming this interesting species for my friend Herbert L. Mason, of the University of California, who also has collected it in the region of Magdalena Bay. Dr. Mason, however, might prefer to consider *A. masonii* as a subspecies of *A. albicans,* since the two populations, undeniably closely related in my opinion, have such similar, twiggy aspects and the structure of the flowers are not too easily distinguishable; then, too, *A. masonii* is restricted to a very limited area around Magdalena Bay and its off-shore islands, at the southern extremity of *A. albicans* but still within its borders. Much the same situation obtains with regard to *A. subaphylla* which also is very closely related, and restricted to a rather narrow area on the eastern shore of the Gulf of California.

The general situation of these three populations is rather similar to that of the subspecies of *A. cryptoceras* and *A. californica,* where, however, the populations are isolated geographically and when not so isolated (viz. *A. cryptoceras* in eastern California) tend to merge. At least in the case of *A. albicans* and *A. masonii,* on the other hand, geographic barriers apparently do not exist and still the populations seem to maintain their integrity, as I judge from the several collections before me.

67. ASCLEPIAS **subaphylla** Woodson, spec. nov.

Frutices vel suffrutices ca. 2–4 m. alti. Caules graciles albescentes juventate minutissime puberuli tandem glabrati aliquando compositi post aetatem florentem aphylli. Folia opposita sessilia linearia 5–8 cm. longa 1–2 mm. lata mox caduca. Inflorescentiae e nodis superioribus laterales brevissime pedunculatae pluriflorae; pedunculis ca. 1.0–1.5 cm. longis minute puberulis; pedicellis gracilibus ca. 1.5 cm. longis. Flores mediocres; calycis laciniis ovato-lanceolatis ca. 3 mm. longis; corolla gilva, lobis ca. 7 mm. longis; gynostegio breve stipitato gilvo vel lacteo, columna latissime obconico ca. 1 mm. longo 2 mm. lato, cucullis obovatis emarginatis patulis ca. 3.5 mm. longis, cornu valde adnato latissime falciformi crista posteriore munito inflexo cucullos superante, androecio late truncateque conico ca.

2 mm. longo 3 mm. lato. Folliculi vel erecti vel subpendentes pedunculis vel erectis vel patulis anguste fusiformes longe apiculati 8–12 cm. longi 1.0–1.5 cm. crassi minutissime puberuli mox glabrescentes; seminibus ovalibus ca. 5 mm. longis, coma pallide lutea ca. 2 cm. longa.—Holotypus: *J. N. Rose, Paul C. Standley & P. G. Russell 14817* in Herb. U. S. Nat. Mus. (Sand dunes, in the vicinity of Altata, Sinaloa, Mexico, April 18, 1910).

Sand dunes and shaded rocky places, Coastal Sinaloa. Blooming from February to September.

MEXICO: SINALOA: Altata, Pueblo del Limón, San Ignacio.

This species, like the preceding *(A. masonii)*, is very closely related to *A. albicans*. The leaves of *A. subaphylla* appear to be larger and maintained longer upon the stems than in either of the two other species. Narvaez Montes and Salazar (sub no. *139* in U. S. Nat. Herb.) report that the species is known as ***candelilla bronca,*** and that the milk is used in villages as a purgative, "the dose a single drop." I cannot decide from the several specimens before me whether the follicles are pendulous or erect; the peduncles appear as erect or ascending.

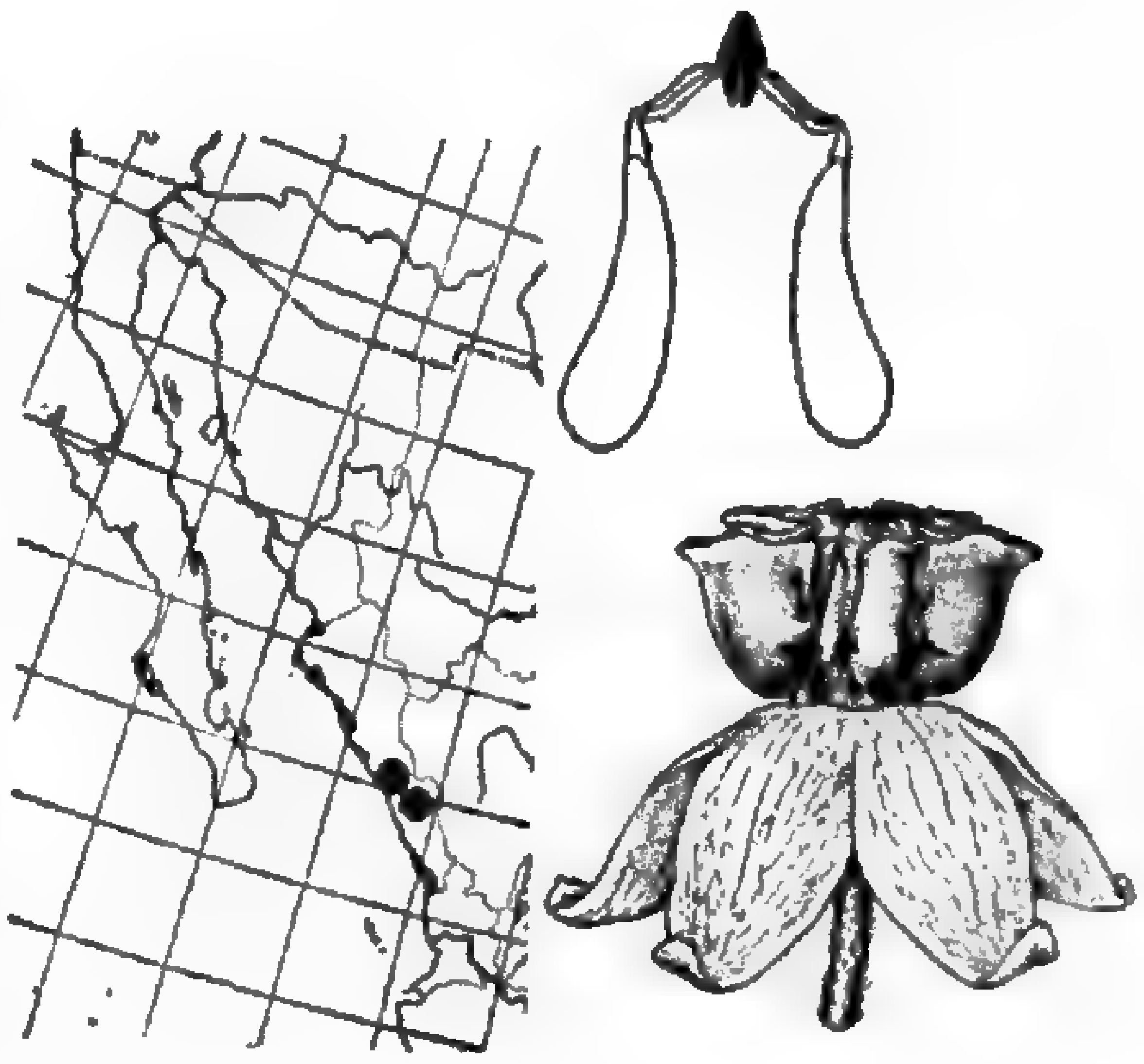

Fig. 73. *Asclepias subaphylla* Woods.

68. ASCLEPIAS ALBICANS S. Wats. in Proc. Amer. Acad. 24:59. 1889. [T.: *E. Palmer 588,* GH!]

Twiggy shrubs. Stems rather slender, simple or repeatedly branching, 1–3 m. tall, heavily glaucous and secreting a thin flaky wax, leafless except on very young growth. Leaves opposite or ternate, linear-filiform, 1–3 cm. long and less than 1 mm. broad, caducous before flowering. Inflorescences terminal and lateral at the uppermost nodes, several- to many-flowered; peduncles 1–3 cm. long, minutely puberulent; pedicels 1–2 cm. long, minutely puberulent. Flowers rather mediocre; calyx lobes ovate, about 3 mm. long, minutely tomentulose; corolla reflexed-rotate, pale yellowish, greenish, or pinkish white, the lobes 6–7 mm. long; gynostegium shortly stipitate, greenish cream or white, rarely tinged with rose, the column rather narrowly obconic, about 1.5 mm. long and 2 mm. broad, the hoods subsaccate, pouched at the base above the basal attachment, deeply emarginate above, 2–3 mm. long, the horn almost wholly coalesced with the body of the hood, free and incurved above, about half longer than the hood, the anther head truncately conic, about 2 mm. long and 3.5 mm. broad. Follicles pendulous on spreading or pendulous peduncles, narrowly fusiform, long-apiculate, 9–13 cm. long, about 1 cm. broad, smooth, minutely pilosulose when young, soon glabrate; seeds oval, about 6 mm. long, the pale tawny coma about 2 cm. long.

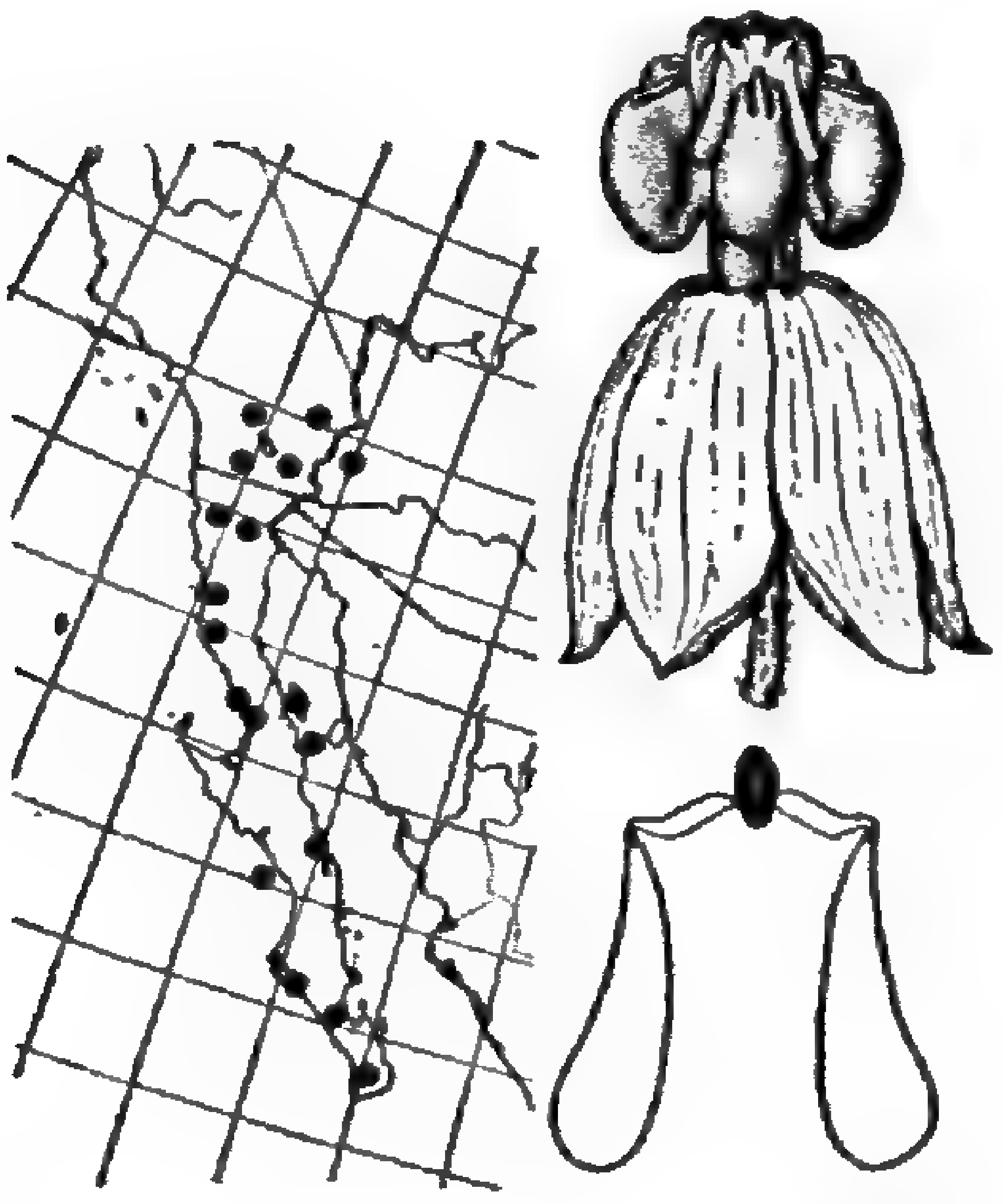

Fig. 74. *Asclepias albicans* S. Wats.

Granite soil, sunny exposures, Colorado Desert and Lower Sonoran. Southern California and adjacent Arizona; Baja California. Blooming from March to June.

United States:

Arizona: Yuma County.

California: Imperial, Riverside, San Bernardino, and San Diego counties.

Mexico: Baja California: Carmen Island, Angel de la Guardia, La Paz, Agua Caliente, Santa Rosalía, San Francisco Island, Los Angeles Bay, Pt. San Fermin Mtns., San Luis Gonzaga Bay, Tule Mtns., Ensenada, San Felipe Bay, Canyon de los Muertes, El Marmol, Puerto Escondido, South San Lorenzo Island.

Probably the shrubbiest American milkweed. The relations of this species with *A. masonii* and *A. subaphylla* are discussed under the former.

69. **Asclepias vestita** Hook. & Arn. Bot. Beechey Voy. 363. 1841. [T.: *Douglas s. n.*, K!]

Herbaceous perennials. Stems clustered from the rootstalk, ascending or more or less decumbent, relatively stout, more or less ancipitous or laterally compressed, simple or infrequently branching from the base, 2–7 dm. long, more or less densely arachnoid-tomentose particularly when young, eventually glabrate. Leaves opposite, shortly petiolate, broadly ovate to ovate-elliptic or broadly lanceolate, apex acuminate, base broadly rounded and usually cordate, 4–14 cm. long, 2–5 cm. broad, firmly membranaceous and sometimes somewhat subsucculent, conspicuously arachnoid-tomentose generally when young, particularly beneath, eventually more or less glabrate; petioles 0.4–1.0 cm. long. Inflorescences terminal and solitary or also lateral at the uppermost nodes, several- to many-flowered, sessile or subsessile even when terminal; pedicels slender, 2–3 cm. long, minutely white-tomentulose. Flowers mediocre; calyx lobes lanceolate, 4–5 mm. long, minutely tomentulose; corolla reflexed-rotate, yellowish white usually more or less suffused with purple, the lobes 7–8 mm. long; gynostegium shortly stipitate, white to cream, the column broadly obconic, about 1 mm. long and 2 mm. broad, the hoods trigonal-obovate, truncate, 2–3 mm. long, the horn falciform, strongly adnate, incurved, about as long as the hood, the anther head truncately conic, about 2 mm. long and 3 mm. broad. Follicles erect on deflexed pedicels, broadly fusiform, shortly apiculate, 5–8 cm. long, about 3 cm. thick, arachnoid-tomentose to glabrate, smooth; seeds broadly oval, about 1 cm. long, the pale tawny coma about 2.5 cm. long.

KEY TO THE SUBSPECIES

Stems relatively stout; leaves larger; inflorescences usually lateral as well as terminal; corolla usually yellowish white or only slightly purplish. Central California............69a. *A. vestita vestita*

Stems relatively slender; leaves smaller; inflorescences usually terminal and solitary; corolla usually deeply suffused with purple. Southern California...............................69b. *A. vestita parishii*

These two populations are not quite as well defined as other subspecies of *Asclepias*, and in such a small area as the species inhabits the intergradation may be environmental rather than genetic. Nevertheless, there is a rather strong geographical correlation.

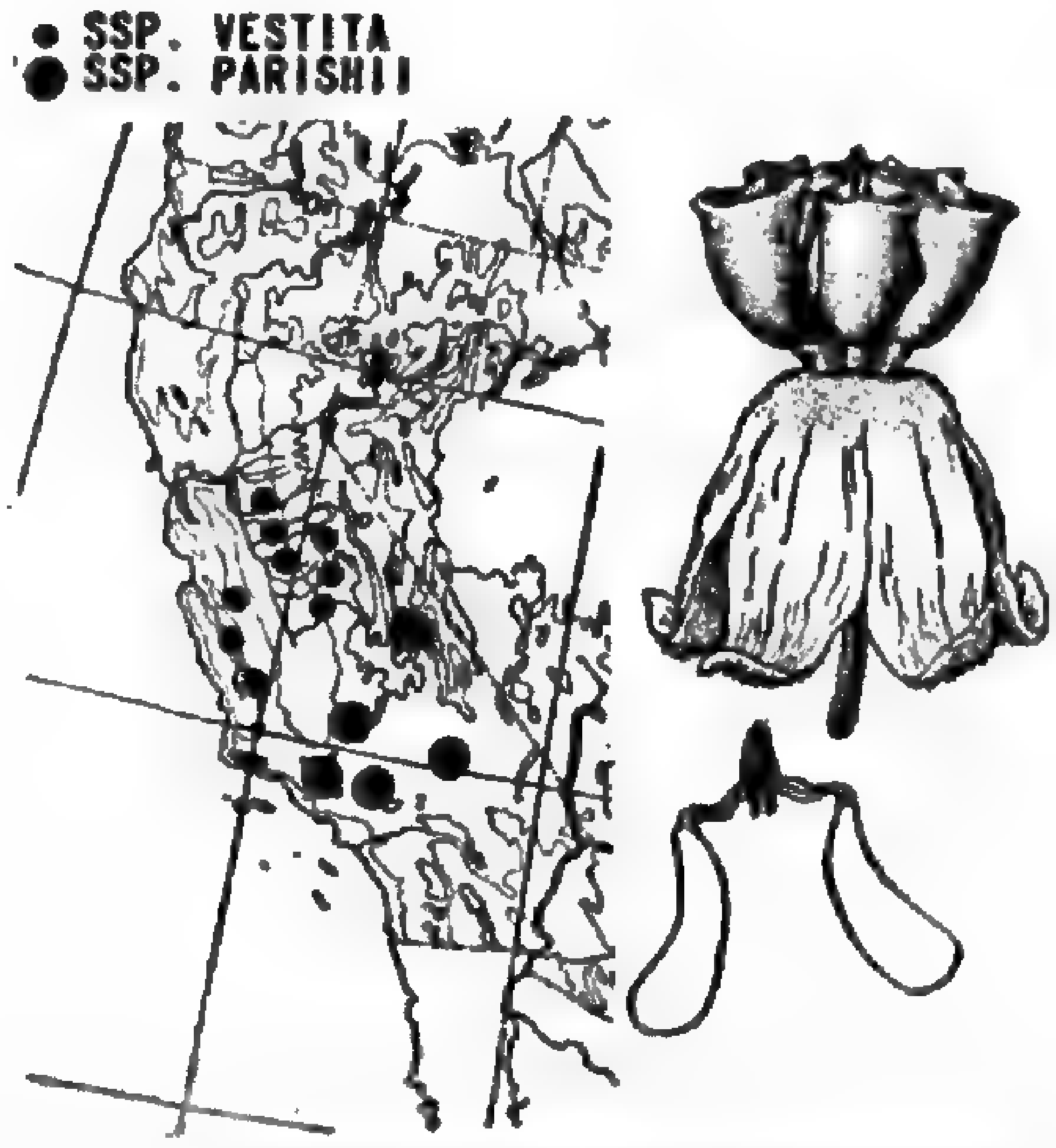

Fig. 75. *Asclepias vestita* Hook. & Arn.

69a. Asclepias vestita ssp. vestita.

Dry plains and low hills. Central California. Blooming from April to July.

United States:

california: Fresno, Madera, Mariposa, Merced, Monterey, San Benito, San Joaquin, and San Luis Obispo counties.

69b. Asclepias vestita ssp. **parishii** (Jepson) Woodson, stat. nov.

Asclepias vestita var. *parishii* Jepson, Man. Fl. Pl. Calif. 772. 1925. [T.: *Jepson 6116*, UC!]

Brushy flats and hillsides, desert canyons. Southern California. Blooming from April to May.

United States:

california: Inyo, Kern, Los Angeles, San Bernardino, and Ventura counties.

70. Asclepias nummularia Torr. Bot. Mex. Bound. Surv. 163, *t. 45*. 1859. [T.: *Bigelow s. n.*, US!]

Diminutive herbaceous perennials, more or less subscapose in appearance because of the decumbent habit and the long peduncles. Stems usually clustered from the rootstalk, decumbent to ascending, usually frequently branched, rarely simple, relatively slender and apparently more or less ancipitous or laterally compressed, 4–10 cm. long, finely tomentulose above to glabrate below. Leaves opposite, subsessile or very shortly petiolate, very broadly ovate or suborbicular to ovate-lanceolate, apex broadly rounded to acute, base broadly rounded and somewhat cordate to obtuse, 1.5–4.0 cm. long, 1–4 cm. broad, firmly membranaceous or somewhat subsucculent, more or less glaucous, finely subarachnoid-tomentulose particularly beneath, infrequently glabrate. Inflorescences terminal and subterminal at the uppermost nodes, few- to several-flowered, long-pedunculate, minutely tomentulose; peduncles 2–6 cm. long, slender; pedicels very slender, 1.5–3.0 cm. long. Flowers rather small; calyx lobes ovate, about 2 cm. long, purplish, finely pilosulose; corolla reflexed-rotate, purplish rose, the lobes about 5 mm. long; gynostegium pale rose, shortly stipitate, the column broadly obconic, about 0.5 mm. long and 2.5 mm. broad, the hoods broadly obovate, broadly obtuse or rounded at the tip, about 3 mm. long, the horn strongly adnate, very broadly falciform or reduced to a rather low crest about as long as the hood or somewhat shorter, the anther head truncately conic, 2.0–2.5 mm. long, 3.0–3.5 mm. broad. Follicles erect on deflexed pedicels, very broadly fusiform, shortly apiculate, 5–6 cm. long, 1.5–2.0 cm. broad, smooth,

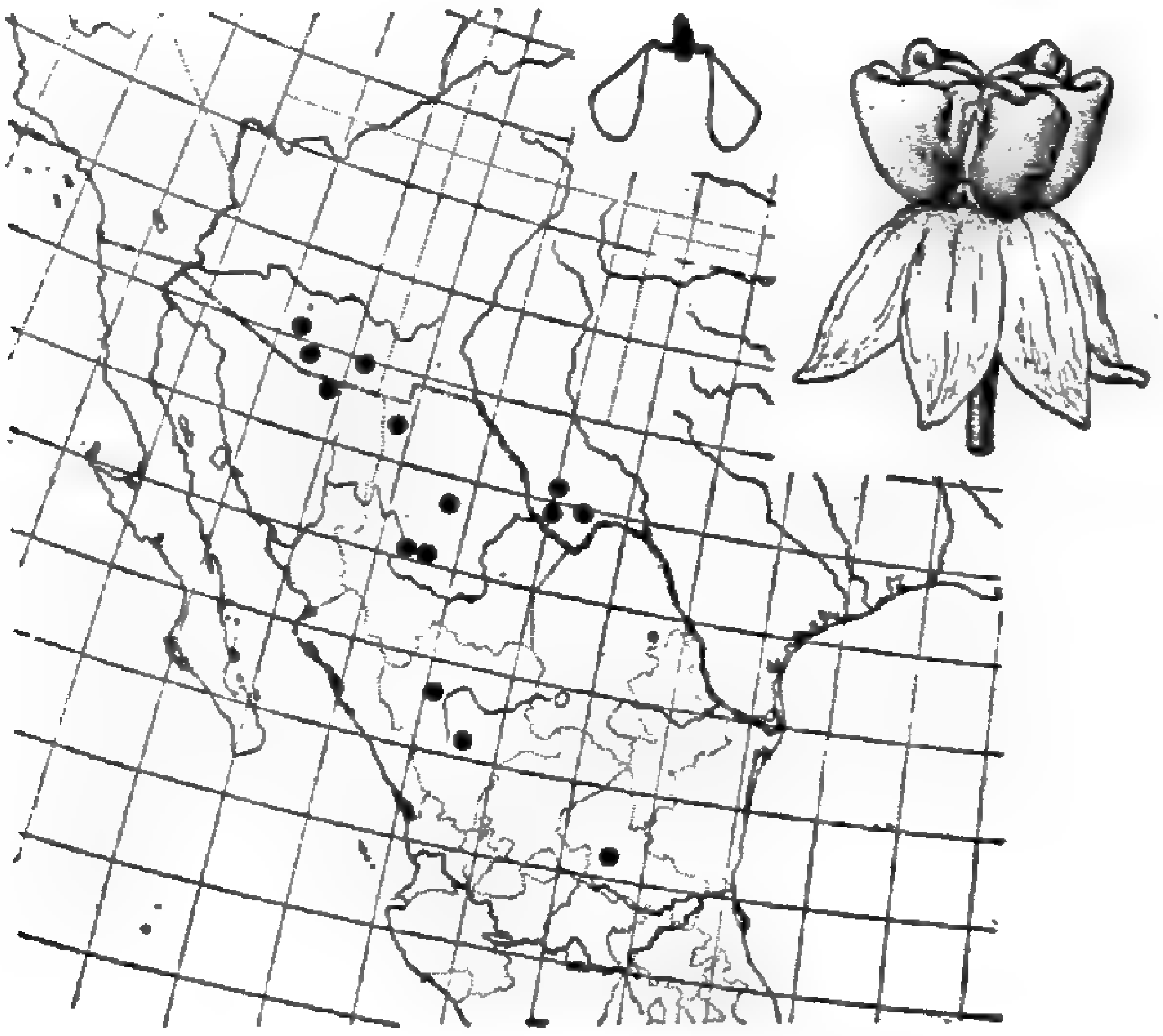

Fig. 76. *Asclepias nummularia* Torr.

finely tomentulose to glabrate; seeds oval, about 6 mm. long, the pale tawny coma about 2.5 cm. long.

Rocky hillsides, arid grassland, dry ravines, in gravel or clay. Southwestern Texas and southern Arizona; northern Mexico from San Luis Potosí to Sonora. Blooming from March to August.

United States:
arizona: Cochise, Pima, and Santa Cruz counties.
texas: Brewster, Jeff Davis, and Presidio counties.

Mexico: chihuahua: Chihuahua, Cusihuiriachic, San Luis Mtns., Hacienda de San Diego, Miñaca. durango: Durango, Tepehuanes. san luis potosí: San Luis Potosí. sonora: Nogales.

A popular name reported from Chihuahua is *yerba de cuervo.*

71. **Asclepias rosea** HBK. Nov. Gen. 3:189. 1819. [T.: *Bonpland 3926,* MO, photo!]

Asclepias senecionifolia M. E. Jones, Contr. West. Bot. 12:49. 1908. [T.: *Jones s. n.,* MO!]

Slender herbaceous perennials from thickened fusiform rootstalks. Stems clustered from the rootstalk, ascending or decumbent, slender, simple or branching from the base, about 0.5–5.0 dm. tall, finely subarachnoid-tomentulose to glabrate. Leaves opposite, sessile, linear to filiform, gradually acuminate, 4–18 cm. long, 3–6 mm. broad, firmly membranaceous, subarachnoid-tomentulose to glabrate. Inflorescences terminal and solitary or lateral also at the upper nodes, several- to many-flowered, finely tomentulose, long-pedunculate; peduncles slender, 2–24 cm. long; pedicels very slender, about 2 cm. long. Flowers small; calyx lobes lanceolate, 2–3 mm. long, finely tomentulose; corolla reflexed-rotate, rather pale purplish pink, the lobes 5–7 mm. long; gynostegium shortly stipitate, rose or pinkish cream, the column broadly obconic, about 0.7 mm. long and 1.5 mm. broad, the hoods broadly obovate, obtuse or rounded at the tip, about 3 mm. long, the horn strongly adnate, broadly falciform, about as long as the hood or somewhat shorter, the anther head

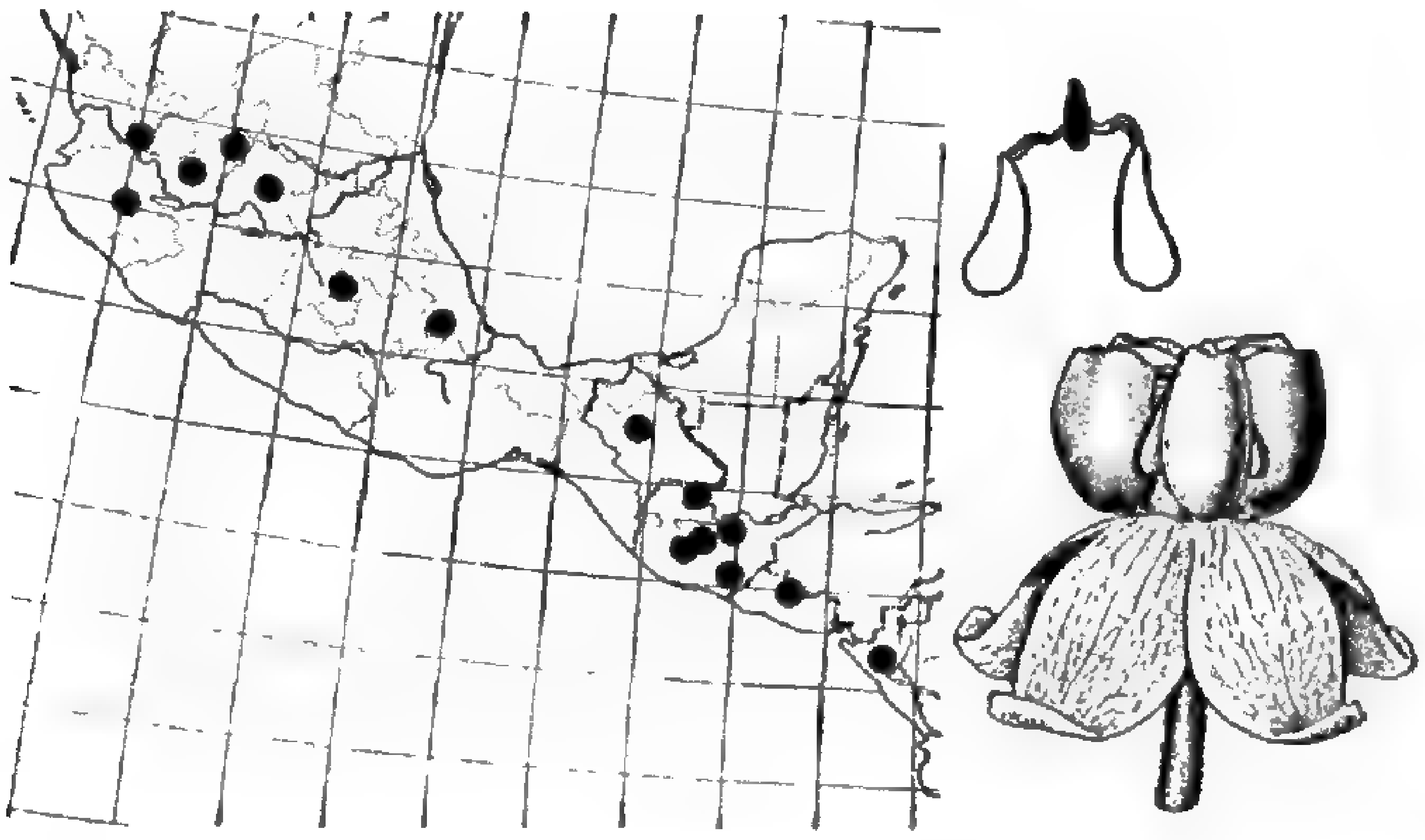

Fig. 77. *Asclepias rosea* HBK.

truncately conic, 1.5–2.0 mm. long, 2.5–3.0 mm. broad. Follicles erect on deflexed pedicels, very narrowly fusiform, narrowly attenuate, 10–15 cm. long, somewhat less than 1 cm. broad, finely tomentulose to glabrate, smooth; seeds oval, 6–8 mm. long, the pale tawny coma about 2.0–2.5 cm. long.

Dry and rocky hills, llanos, and potreros. Southern Mexico and Guatemala. Blooming from December to June.

MEXICO: CHIAPAS: Monserrate. GUANAJUATO: Guanajuato, Silao. JALISCO: Jacala, Guadalajara, Altanguillo, Tapalpa, Santa Cruz. MEXICO: Temascaltepec.

GUATEMALA: CHIMALTENANGO: Alameda. GUATEMALA: Guatemala, Finca La Aurora. QUICHE: locality lacking. SANTA ROSA: Estanzuela, Santa Rosa. SOLOLA: Volcán San Pedro.

Popular names reported in Guatemala are *platanillo* and *bonetillos,* and in Mexico the usual *lechetresna.*

Series 9. FRUTICOSAE

72. ASCLEPIAS FRUTICOSA L. Sp. Pl. 216. 1753. [T.: Linn. Herb., London, no. *310.23*, photo!]

Gomphocarpus fruticosus (L.) R. Br. in Mem. Wern. Soc. 1:38. 1809.
Gomphocarpus angustifolius Link, Enum. Hort. Berol. 1:251. 1821–22, ex char.
Gomphocarpus arachnoideus Fourn. in Bull. Soc. Bot. France 14:250. 1867, ex char.
Gomphocarpus brasiliensis Fourn. in Mart. Fl. Bras. 6^4:203, *pl. 53.* 1885, ex ic. [T.: *Glaziou 6706.*]
Gomphocarpus fruticosus f. *brasiliensis* (Fourn.) Briq. in Kgl. Sv. Vet. Akad. Handl. 34^7:21. 1900.
Asclepias brasiliensis (Fourn.) Schltr. in Mededel. Rijks Herb. 29:12. 1916.

Stout suffrutescent perennials. Stems relatively stout, branching rather frequently, about 1–2 m. tall, finely puberulent to glabrate. Leaves opposite, subsessile, narrowly lanceolate to oblong-lanceolate, acuminate, base acute, 4–15 cm. long, 1–2 cm. broad, finely pilosulose to glabrate. Inflorescences lateral and solitary from the upper nodes, several-flowered, pedunculate, inconspicuously puberulent; peduncles slender, 2–3 cm. long; pedicels very slender, about 2 cm. long. Flowers rather large; calyx lobes lanceolate, 2–3 mm. long, minutely puberulent; corolla reflexed-rotate, white, the lobes 7–8 mm. long; gynostegium rather shortly stipitate, cream or white flushed with purple or violet, the column obconic, about 2 mm. long and 3 mm. broad, the hoods strongly conduplicate, broadly lyriform with 2 conspicuous falciform lobes, about 3 mm. long, without a horn, the anther head truncately conic, about 2 mm. long and 3 mm. broad. Follicles erect on deflexed pedicels, broadly ovoid, 5–8 cm. long, minutely puberulent, closely beset with slender filiform spines.

Waste places particularly about dwellings; sporadically introduced into Jamaica and South America from Africa. Blooming from December to July.

To be complete, the synonymy probably should include a number of names from Africa, notably *Gomphocarpus physocarpus* E. Mey. Although I have seen no specimens from Mexico, Fournier's description of *Gomphocarpus arachnoideus*, which was described from horticultural material supposedly from Mexico, seems to apply to this species. I have not been able to see the type. Similarly, Fournier's G. *brasiliensis*, which is illustrated by an excellent plate in Martius' 'Flora Brasiliensis', is surely the African species. Although introduced into America for at least a century, *A. fruticosa* has not spread greatly and still is collected very infrequently.

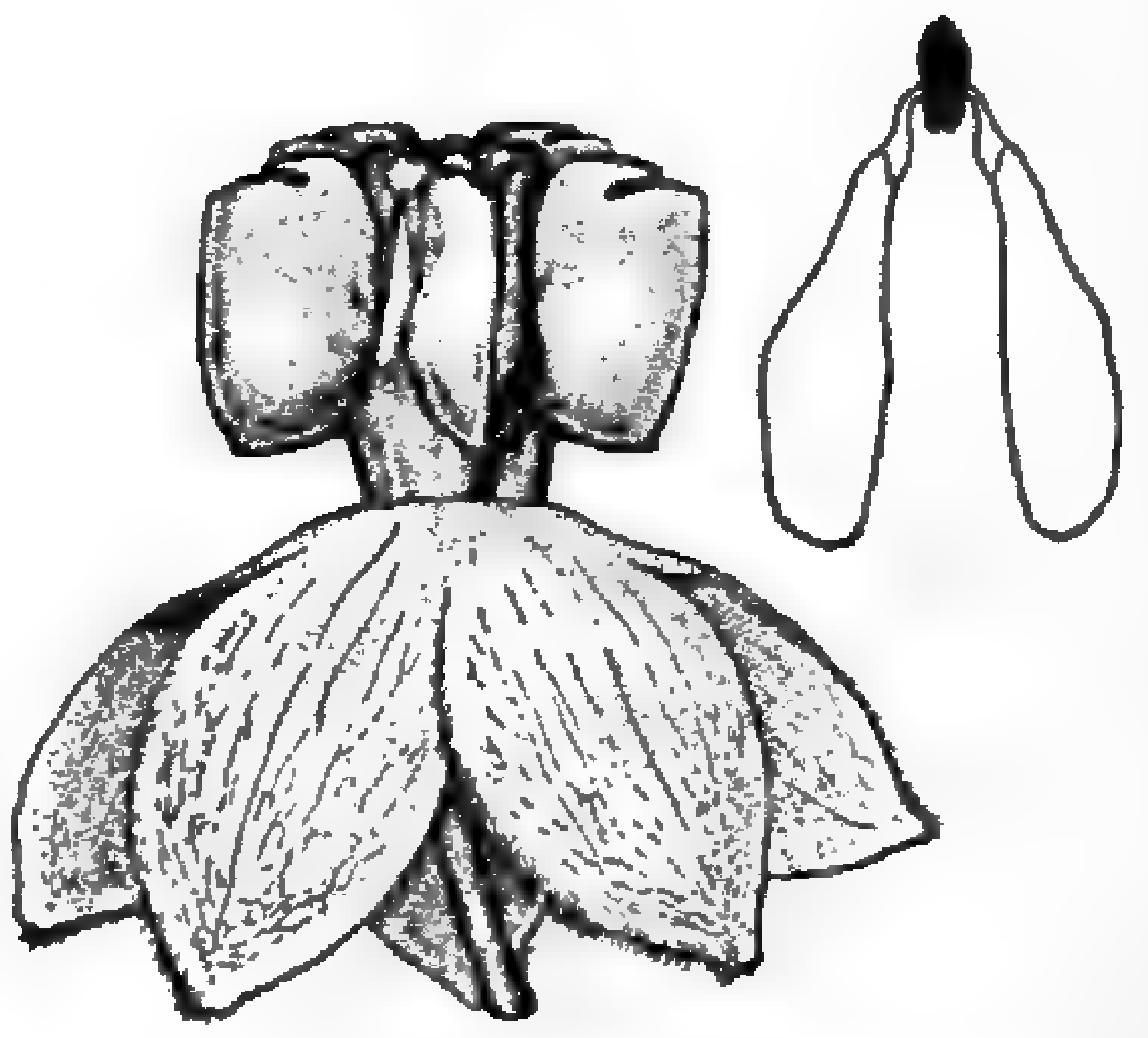

Fig. 78. *Asclepias fruticosa* L.

SUBGENUS II. PODOSTEMMA (Greene) Woodson, stat. nov.

Podostemma Greene, Pittonia 3:235. 1897. [T.: *P. longicornu* (Benth.) Greene.]

KEY TO THE SPECIES

a. Anther wings salient at the base; inflorescences definitely pedunculate.
  b. Plants herbaceous; leaves broadly laminate, persistent; flowers relatively large, the corolla lobes about 1.5 cm. long; hoods somewhat attenuate to the tip, with 2 very prominent laminate auricles at the base; horns narrowly clavate, attached about midway within the hoods. Jalisco to Chiapas; Guatemala.......................................73. *A. auriculata*
  bb. Plants suffruticose; leaves filiform and soon caducous; flowers smaller, the corolla lobes about 1 cm. long; hoods dilated at the tip, rather inconspicuously carinate at the base; horns reduced to rather inconspicuous crests almost wholly adnate to the hoods; follicles pendulous or subpendulous. Southern California and adjacent Arizona and Nevada; Baja California and coastal Sonora and Sinaloa.......................................74. *A. subulata*
aa. Anther wings salient at about the middle; inflorescences typically sessile or subsessile.
  b. Hoods at least two to three times as long as the anther head.
    c. Hoods somewhat spreading at the tips, broadly rounded to somewhat quadrangular, entire to slightly emarginate, the horn not quite wholly adnate; flowers relatively large, the corolla lobes typically somewhat longer than 1 cm.
      d. Hoods about three times as long as the anther head, not attenuate toward the base. Southern New Mexico and Arizona and adjacent California..............75. *A. nyctaginifolia*
      dd. Hoods about twice as long as the anther head, conspicuously attenuate toward the base. Southwestern Texas and southern New Mexico; Tamaulipas to Chihuahua and southward to Yucatan and Chiapas; Guatemala; Honduras; El Salvador; Nicaragua; Costa Rica ....76. *A. oenotheroides*
    cc. Hoods essentially erect, the tip deeply 2-lobed, the horn adnate to the sinus and enclosing the hood from above; flowers smaller, the corolla lobes typically somewhat less than 1 cm. long. Southwestern Texas; northern Nuevo León and Tamaulipas ....77. *A. emoryi*
  bb. Hoods about as long as the anther head or only slightly longer; flowers relatively small, the corolla lobes about 7 mm. long. Sinaloa ....78. *A. standleyi*

This is a fairly natural group of species, with the exception of *A. auriculata* which might at least be included within a series of its own apart from the rest. Nevertheless, *A. obovata* of subgenus ASCLEPIAS approaches PODOSTEMMA rather closely (particularly *A. nyctaginifolia*), and the hoods of *A. standleyi* are so short that it has little in general appearance of the flower to ally it with the others.

73. ASCLEPIAS AURICULATA HBK. Nov. Gen. 3:191, *t. 228*. 1819, ex ic. [T.: *Bonpland s. n.*]

Otaria auriculata (HBK.) G. Don, Gen. Syst. 4:144. 1838.
Otaria fragrans Benth. Pl. Hartw. 89. 1842. [T.: *Hartweg s. n.*, MO photo!]
Asclepias fragrans (Benth.) Dcne. in DC. Prodr. 8:571. 1844.
Asclepias mazatlanensis Sessé & Moc. La Naturaleza Ser. II, 1:app. 43. 1887. [T.: *Sessé & Mociño 843*, F!]
Asclepias purpusii Brandg. in Zoe 5:251. 1908. [T.: *Purpus 2099*, MO!]
Asclepias plumerifolia Goyena, Fl. Nicaraguense 2:658. 1911, ex char.

Stout herbaceous perennials. Stems relatively stout, simple, 6–20 dm. tall, inconspicuously puberulent above, eventually glabrate. Leaves opposite, shortly petiolate, elliptic to oblong, apex rather shortly acuminate, base acute to obtuse, 10–15 cm. long, 1.5–6.0 cm. broad, thinly membranaceous, dark green and essen-

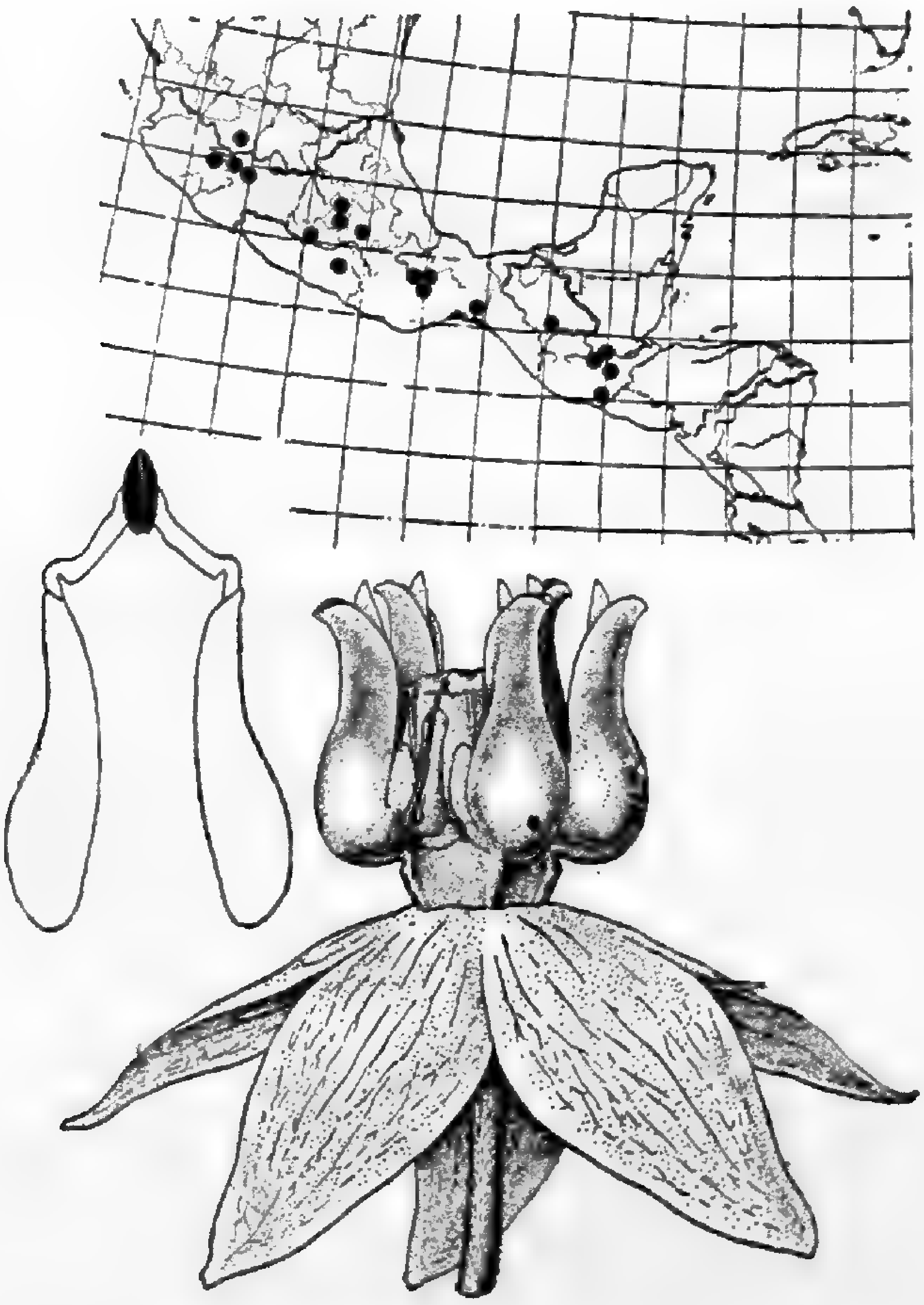

Fig. 79. *Asclepias auriculata* HBK.

tially glabrous above, paler and inconspicuously puberulent beneath; petioles 0.4–1.0 cm. long. Inflorescences subterminal and lateral at the upper nodes, few to several, rather shortly pedunculate, several- to many-flowered; peduncles rather slender, 3–5 cm. long, inconspicuously puberulent; pedicels rather slender, 2.5–3.0 cm. long, minutely puberulent. Flowers large; calyx lobes lanceolate, 7–8 mm. long, usually dark purple, minutely puberulent; corolla rotate or reflexed-rotate, greenish white sometimes tinted with rose at the base, the lobes 1.2–1.5 cm. long; gynostegium shortly stipitate, white to pale lavender or rose, the column broadly obconic, about 4 mm. long and 5 mm. broad, the hoods ovate-oblong, 7–10 mm. long, the base enlarged and spongy-solid, auriculate at the base, the tip somewhat narrowed and laminate, the horn about half adnate and confluent with the base, compressed-clavate, about as long as the hood or somewhat shorter, the anther head cylindrical, about 4 mm. long and broad. Follicles unknown.

Rocky hills, open pine and oak forests. Southern Mexico; Guatemala. Blooming from June to October.

MEXICO: CHIAPAS: Tonala, Mt. Tacana. GUERRERO: Mina, Aguazarca, Cuchara. JALISCO: San Sebastián, Arroyo Seco, Sierra de la Campana, Sierra del Tigre, Guadalajara. MEXICO: Temascaltepec. MICHOACAN: Uruapán. MORELOS: Cuernavaca, Herradura. OAXACA: Cerro San Felipe, Nochixtlán, Jayacatlán. PUEBLA: Pahuatlân.

GUATEMALA: GUATEMALA: Guatemala, La Aurora, San Juan Sacatepequez. SANTA ROSA: Carrizal. ZACAPA: Sierra de las Minas.

I am embarrassed not to be able to describe the fruit of *A. auriculata;* for such a relatively frequent and widely distributed species fruit must have been collected. As it happens, *A. similis,* which has nearly the same distribution, looks almost precisely like *A. auriculata* when not in flower, and I am sure that I must have wrongly identified some fruiting plants of the latter species with the name of the former.

74. ASCLEPIAS SUBULATA Dcne. in DC. Prodr. 8:571. 1844. [T.: Herb. Pavon, Fl!]

Slender twiggy undershrubs, somewhat resembling an Ephedra. Stems clustered from the base, slender, simple or branching, about 1–2 m. tall, leafless except when very young, glabrous. Leaves opposite or ternate, caducous before flowering, sessile, linear or filiform, 2–8 cm. long, about 1–2 mm. broad. Inflorescences lateral from few to several of the upper nodes, few- to several-flowered, shortly pedunculate; peduncles relatively stout, 1–2 cm. long, very minutely puberulent; pedicels more slender, 1.0–1.5 cm. long, minutely puberulent. Flowers rather large; calyx lobes lanceolate, about 3 mm. long; corolla reflexed-rotate, pale yellowish white, the lobes 9–11 mm. long; gynostegium shortly stipitate, cream, the column broadly obconic, about 1 mm. long and 2.5 mm. broad, the hoods broadly obovate-flabellate, 9–10 mm. long, narrowed to a solid slightly laminate stipe somewhat above midway, the expanded blade acute, emarginate and indefinitely laminate, the horn wholly adnate and reduced to an undulate crest, slightly shorter than the hood, the anther head conic, about 3.0–3.5 mm. long and 4–5 mm. broad. Follicles on pendulous or subpendulous peduncles, narrowly fusiform, narrowly attenuate, 8–14 cm. long,

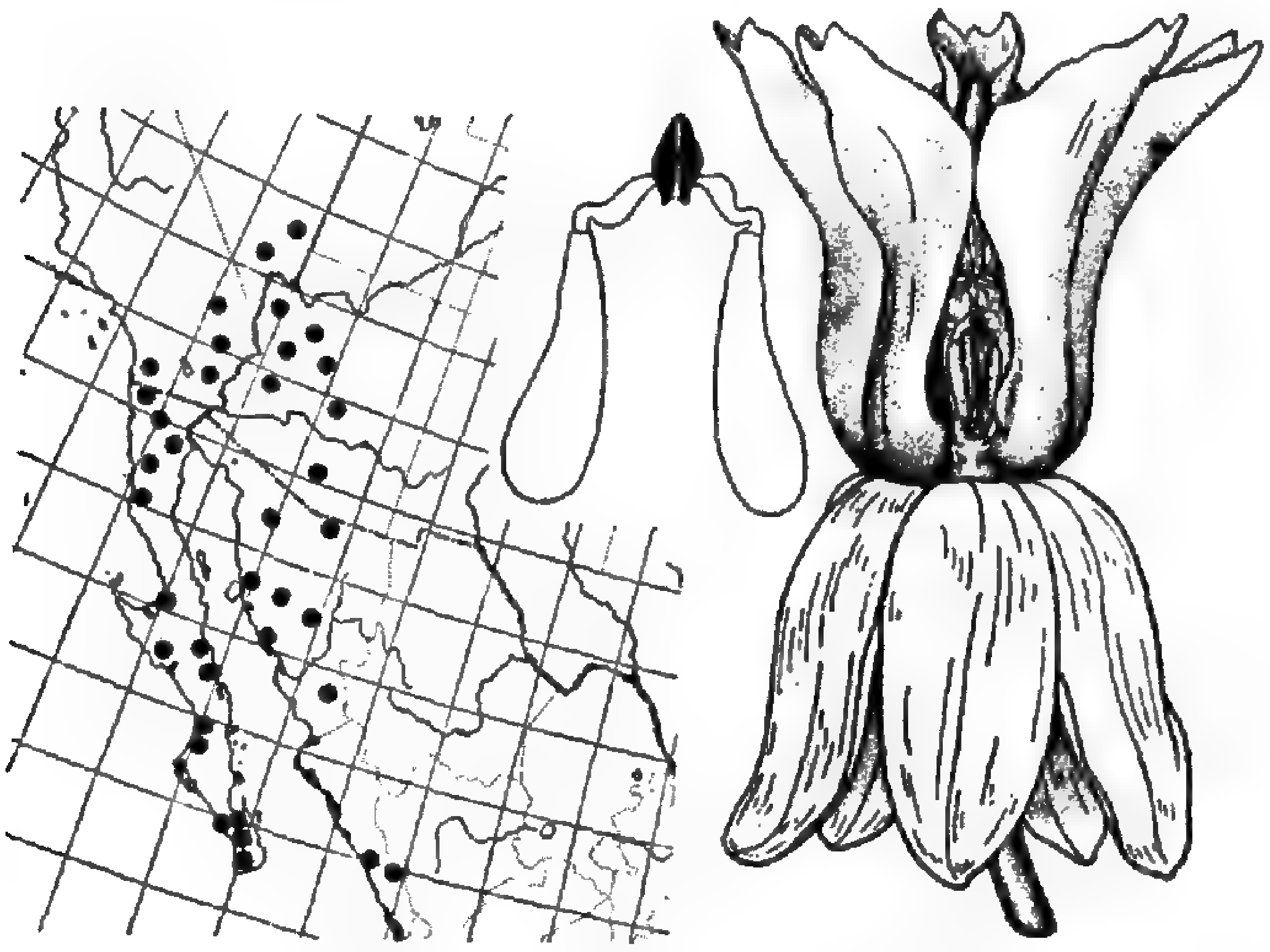

Fig. 80. *Asclepias subulata* Dcne.

about 1 cm. thick, smooth, minutely puberulent to glabrate; seeds oval, about 6 mm. long, the pale tawny coma about 3–4 cm. long.

Deserts, chiefly along arroyos and washes. Southern California and adjacent Arizona and Nevada; Baja California and western Sonora. Blooming sporadically throughout the year.

UNITED STATES:
ARIZONA: Pima, Pinal, Maricopa, Mohave, and Yavapai counties.
CALIFORNIA: Imperial, Riverside, San Bernardino, and San Diego counties.
NEVADA: Clark and Lincoln counties.

MEXICO: BAJA CALIFORNIA: Todos Santos, La Paz, Tijuana, San Isidro Ranch, Santa María Bay, Cape San Lucas, San Juanico Bay, San José del Cabo, Mesquital, Ensenada, Santo Tomás, Ojos Negros, Mulege, San Bartolo, Guadalupe, Santa Rosalía, San Ignacio, San Bartolomé Bay, Rosario, San Felipe Bay, Santo Domingo. SONORA: Guaymas, Quitovac, Hermosillo, Villa Seris, Bahía Kino, Torres Palma, Río Mayo, Nogales, Caborca. SINALOA: San Ignacio, San Blas.

An extremely uniform species as far as floral structure is concerned. The caducous leaves of both *A. subulata* and *A. albicans* may be either opposite or ternate. It is fortunate that plants of both species, as well as those of *A. masonii* and *A. subaphylla*, usually fruit and bloom at the same time, for otherwise they would be almost indistinguishable in fruit.

75. **ASCLEPIAS NYCTAGINIFOLIA** A. Gray, in Proc. Amer. Acad. 12:69. 1877. [T.: *E. Palmer s. n.*, MO!]

Asclepias wrightii Greene, ex A. Gray, in Proc. Amer. Acad. 16:102. 1881. [T.: *C. Wright s. n.*, MO!]
Podostemma nyctaginifolium (A. Gray) Greene, Pittonia 3:237. 1897.

Rather low herbaceous perennials. Stems clustered from the base, ascending or decumbent, relatively slender, simple or rarely branching from the base, 1.5–2.0 dm. tall, finely puberulent. Leaves opposite, long-petiolate, ovate-subrhombic, apex acute to obtuse, base broadly obtuse or rounded and abruptly cuneate into the petiole, 6–10 cm. long, 2–4 cm. broad, membranaceous, finely puberulent particularly beneath; petioles 1–3 cm. long. Inflorescences lateral and solitary at few to several of the upper nodes, few- to several-flowered, sessile or subsessile; pedicels rather stout, about 2 cm. long, finely puberulent. Flowers large; calyx lobes ovate-lanceolate, about 4 mm. long, minutely puberulent. Corolla rotate or reflexed-rotate, pale greenish yellow slightly tinted with purple without, the lobes 1.2–1.4 cm. long; gynostegium shortly stipitate, pale greenish cream, the column shortly obconic, about 0.5 mm. long and 1 mm. broad, the hoods broadly oval or oblong, about 1 cm. long, not noticeably attenuate at the base, the tip rounded and obscurely repand, the horn almost wholly adnate, virtually reduced to a broad apiculate crest, slightly shorter than the hood, the anther head broadly truncate-conic, about 2 mm. long and 3 mm. broad. Follicles erect on deflexed pedicels, broadly fusiform, shortly apiculate, 3–5 cm. long, 1.5–3.0 cm. broad, minutely tomentellous to glabrate; seeds unknown.

Arroyos, springs, and swales. Southern New Mexico and Arizona and adjacent California (New York and Providence mountains). Blooming from May to August.

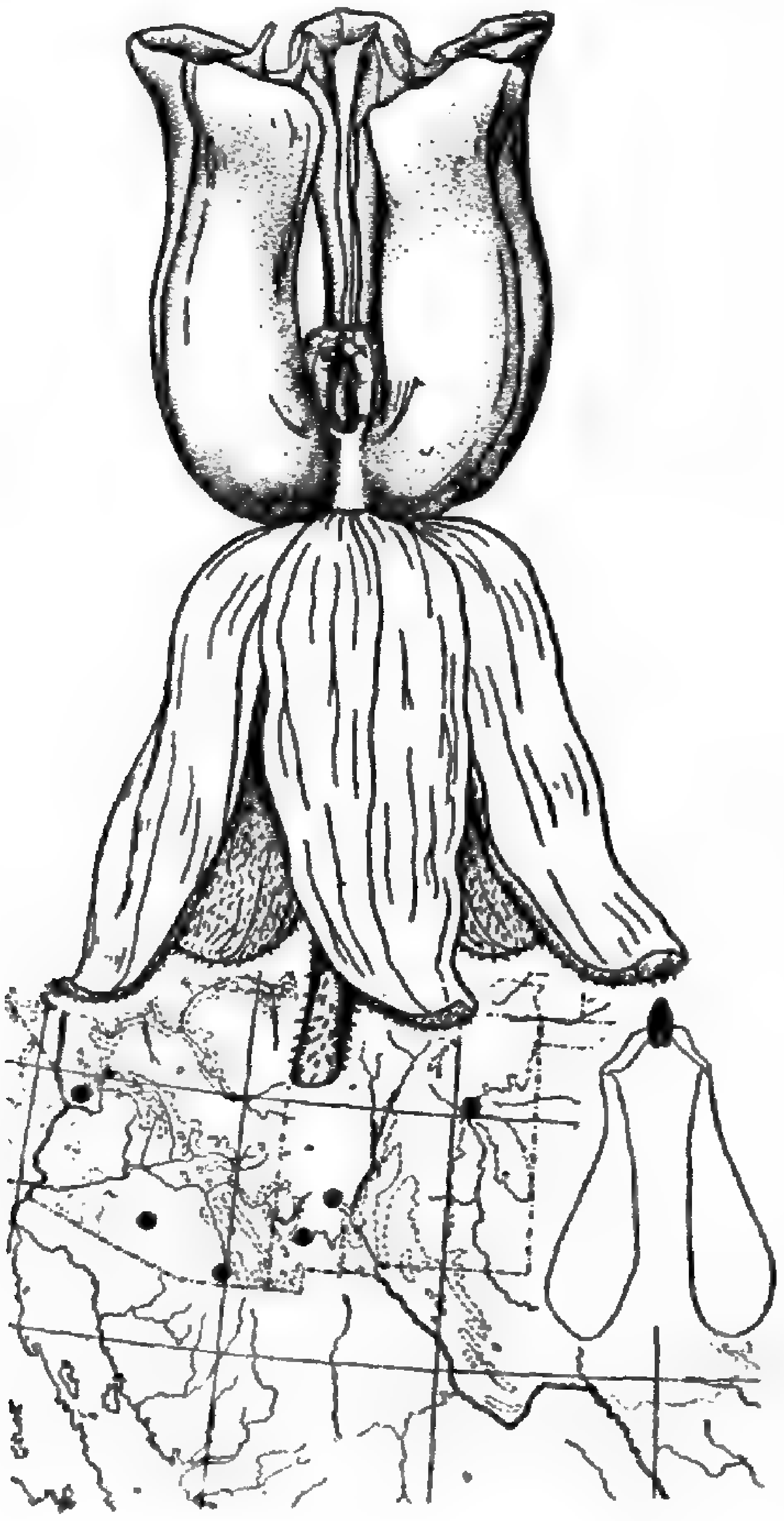

Fig. 81. *Asclepias nyctaginifolia* A. Gray

United States:
ARIZONA: Cochise, Mohave, and Pima counties.
CALIFORNIA: San Bernardino County.
NEW MEXICO: Grant, Guadalupe, and Sierra counties.

76. ASCLEPIAS OENOTHEROIDES Cham. & Schlecht. in Linnaea 5:123. 1830. [T.: *Schiede & Deppe 256*, K!]

Asclepias longicornu Benth. Pl. Hartw. 24. 1839. [T.: *Hartweg 214*, K!]
Asclepias lindheimeri Engelm. & Gray, in Boston Jour. Nat. Hist. 5:250. 1845. [T.: *Lindheimer 272*, MO!]
Asclepias brevicornu Scheele, in Linnaea 21:756. 1848, ex char. [T.: *Roemer s. n.*]
Asclepias amoena R. & P. ex Hemsl. Biol. Centr.-Amer. Bot. 2:325. 1881, nom. nud., non L.
Podostemma lindheimeri (Engelm. & Gray) Greene, Pittonia 3:236. 1897.
Podostemma longicornu (Benth.) Greene, loc. cit. 1897.
Podostemma australe Greene, loc. cit. 238. 1897. [T.: *C. Wright s. n.*, US!]
Podostemma helleri Greene, loc. cit. 236. 1897. [T.: *Heller 1575*, MO!]

Low herbaceous perennials. Stems clustered from the rootstalk, ascending or decumbent, moderately stout, more or less branched from the base or simple, 0.5–4.5 dm. long, minutely puberulent. Leaves opposite, rather long-petiolate, rhombic-ovate to oblong-lanceolate, apex obtuse to acute, base acute to broadly obtuse and abruptly cuneate to the petiole, 4–12 cm. long, 1–6 cm. broad, firmly membranaceous, pale green, minutely puberulent particularly beneath; petioles 1–2 cm. long. Inflorescences lateral and solitary from few to several of the upper nodes, very shortly pedunculate or subsessile, several-flowered; peduncles 1–2 cm. long or nearly obsolete, minutely puberulent; pedicels rather slender, 1.5–2.5 cm. long, minutely puberulent. Flowers mediocre; calyx lobes ovate-lanceolate, 3–4 mm. long, minutely puberulent; corolla reflexed-rotate, greenish white or yellow, the lobes 0.8–1.4 cm. long; gynostegium very shortly stipitate, pale greenish cream, the column broadly obconic, about 1.5 mm. long and 2.5 mm. broad, the hoods narrowly obovate-flabellate, 7–10 mm. long, conspicuously narrowed to a narrowly laminate stipe from somewhat above the middle, the tip broadly laminate and minutely erose or repand, the horn adnate to near the tip of the hood, the free portion falciform and incurved, usually accompanied by a smaller posterior appendage, the anther head truncate-conic, about 3 mm. long and 4–5 mm. broad. Follicles erect on deflexed pedicels, broadly fusiform or ovoid, shortly apiculate, 7–9 cm. long, 1.5–2.0 cm. broad, smooth, minutely pilosulose to glabrate; seeds oval, 6–8 mm. long, the pale tawny coma 2.0–2.5 cm. long.

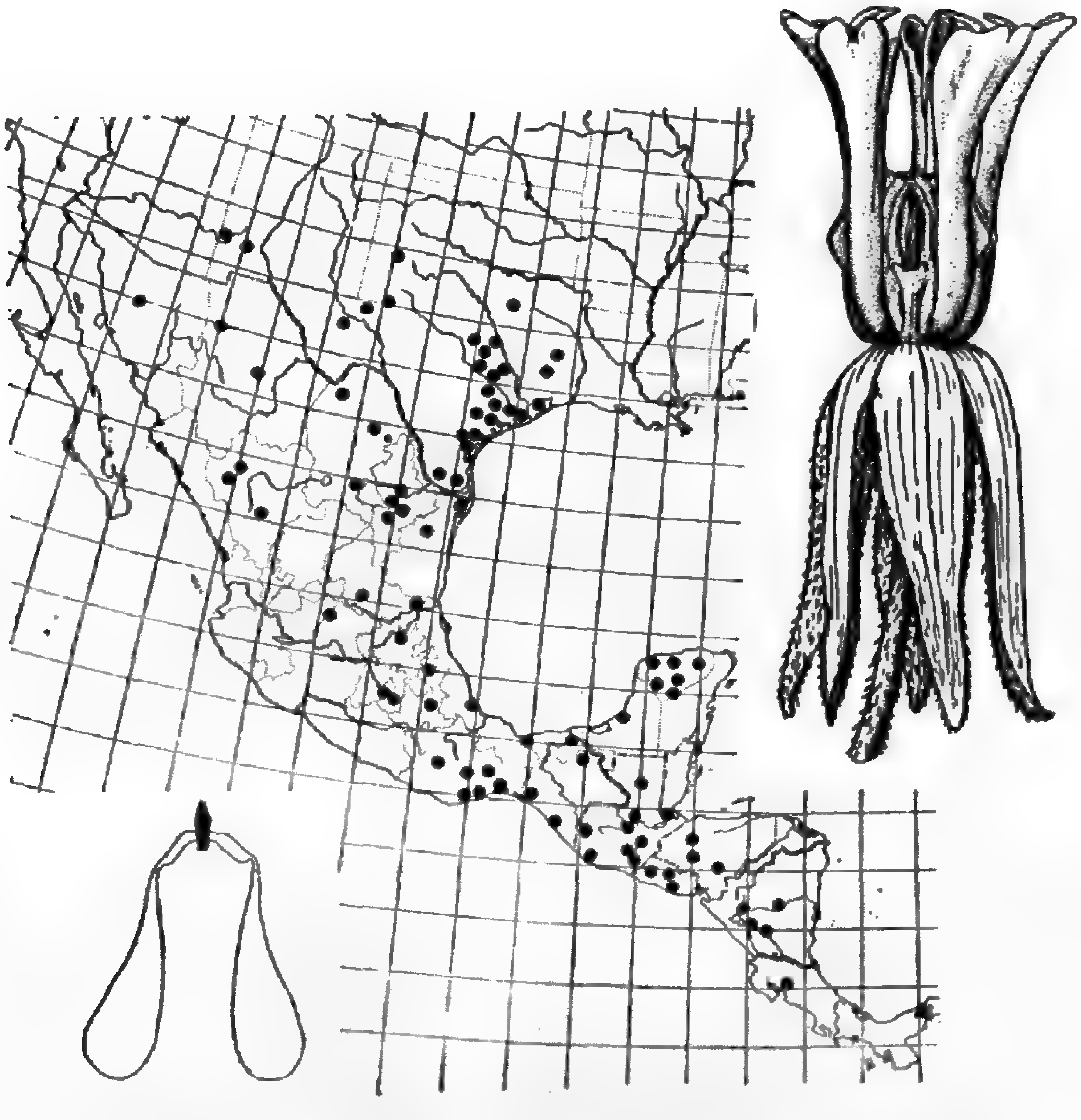

Fig. 82. *Asclepias oenotheroides* Cham. & Schlecht.

Rocky, chiefly clay soil in llanos, mesas, and hills, in fields and thickets, along roadsides. Southern Texas and New Mexico; central Mexico from Tamaulipas to Sonora and southward to Chiapas and Yucatan; Guatemala; Honduras; El Salvador; Nicaragua; Costa Rica. Blooming from February to October.

UNITED STATES:
NEW MEXICO: Chaves, Dona Ana, and Grant counties.
TEXAS: Bastrop, Bell, Burnet, Caldwell, Cameron, Colorado, Crane, Dallas, De Witt, Galveston, Goliad, Gonzales, Grimes, Hays, Hidalgo, Jackson, Jim Wells, Lubbock, Matagorda, Nueces, Pecos, San Patricio, and Travis counties.

MEXICO: CAMPECHE: Champotón. CHIAPAS: Paderon, Tonala, Mapastepec, Monserrate. CHIHUAHUA: Ciudad Jimenez, Chihuahua, Casas Grandes. COAHUILA: Allende, Sabinas, Saltillo, Morano, Puerto Colorado. DURANGO: Santiago Papasquiaro, Tepehuanes, Durango. GUANAJUATO: Irapuato. HIDALGO: Jacala. MORELOS: Cuernavaca, Yautepec. NUEVO LEÓN: Monterrey, Villa Santiago, Sabinas Hidalgo, Galeana. OAXACA: Oaxaca, Totolapán, Soledad de Etla, Tehuantepec, Jamiltepec, San Matéo del Mar. PUEBLA: San Luis Tultitlanapa, Tlacuiloltepec. SAN LUIS POTOSÍ: Chijol, San Luis Potosí, Charcas. SONORA: Magdalena. TABASCO: Estapilla. TAMAULIPAS: Washington Beach, San José. VERACRUZ: Coatzacoalcos, Vera Cruz. YUCATAN: Ticul, Dzitás, Tecantun, Chichen Itza, Mérida, Izamal, Xcabakunché, Progreso, Chichankanab, Valladolid.

GUATEMALA: GUATEMALA: Guatemala. IZABAL: Gualán. JUTIAPA: El Barrial, Atescatempa. PETEN: La Libertad, Tayasal. PROGRESO: El Rancho. RETALHULEU: Champerico, Nueva Linda, Retalhuleu. SAN MARCOS: Ayutla. SANTA ROSA: Chiquimulilla. ZACAPA: Zacapa, La Fragua, Estanzuela, Santa Cruz.

HONDURAS: COMAYAGUA: Comayagua. EL PARAISO: Danlí. MORAZAN: El Zamorano, Tegucigalpa, Toncontín.

EL SALVADOR: AHUACHAPAN: Ahuachapán. LA UNION: La Union. SAN VICENTE: San Vicente. SONSONATE: Sonsonate, Acajutla, Izalco.

NICARAGUA: CARAZO: Jinotepe. CHINANDEGA: Corinto, Chichigalpa, Chinandega. GRANADA: Granada. MANAGUA: Managua.

COSTA RICA: GUANACASTE: Paso Temisque.

Popularly known as *matacoyote* in El Salvador, and *leche perro* in Costa Rica.

The flowers of *A. oenotheroides* are structurally about the most elegantly contrived of all milkweeds, but the color is very dingy and the whole aspect of the plant is extraordinarily weedy.

It is unfortunate to have to displace the familiar name *longicornu* in favor of *oenotheroides*, but there can be no doubt of the necessity for doing so. There is considerable variation in the size of the flowers and also in such structural features as the small posterior horn of the hoods, but I have noticed no geographical pattern. Some of the variation may be due to occasional hybridization with *A. emoryi*.

77. ASCLEPIAS EMORYI (Greene) Vail, ex Small, Fl. Southeast. U. S. 948. 1903.

Podostemma emoryi Greene, Pittonia 3:237. 1897. [T.: *Thurber s. n.*, US!]
Podostemma leoninum Greene, loc. cit. 1897. [T.: *Pringle 2519*, MO!]
Asclepias bartlettiana Woodson, in Amer. Jour. Bot. 22:688, *pl. 1, fig. 3*. 1935. [T.: *Bartlett 10659*, MICH!]

Low herbaceous perennials. Stems usually clustered from the rootstalk, ascending or decumbent, rather slender, more or less branched from the base or simple,

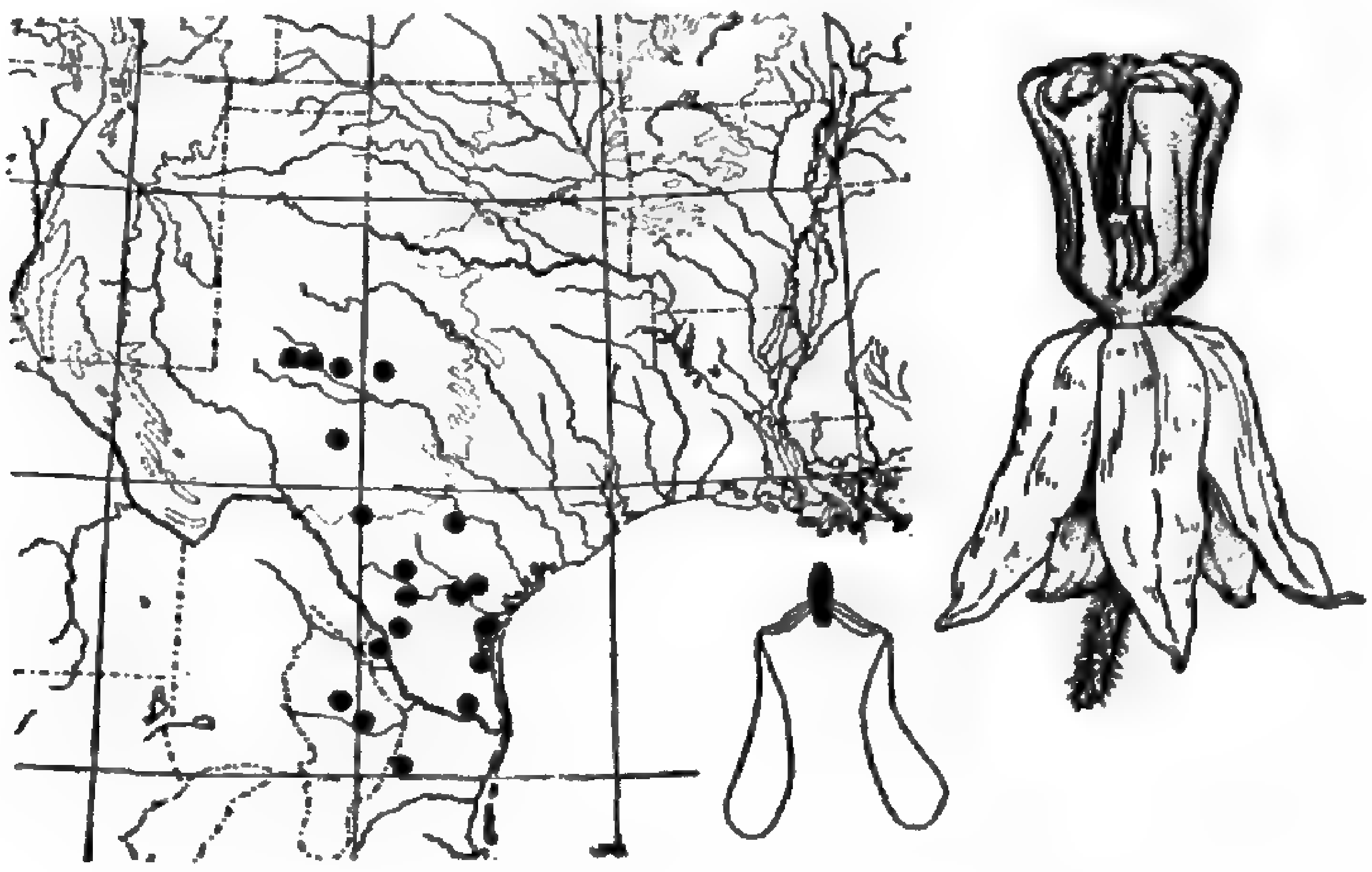

Fig. 83. *Asclepias emoryi* (Greene) Vail

1–2 dm. long, minutely puberulent. Leaves opposite, rather long-petiolate, rhombic-ovate to narrowly oblong-lanceolate particularly above, apex obtuse to narrowly acute, base acute to obtuse and abruptly cuneate into the petiole, 4–8 cm. long, 0.6–4.0 cm. broad, firmly membranaceous, pale green, minutely puberulent particularly beneath; petioles 1.0–1.5 cm. long. Inflorescences lateral and solitary from few to several of the upper nodes, shortly pedunculate to sessile; peduncles obsolete to 2 cm. long, densely puberulent; pedicels rather slender, 1–2 cm. long, minutely puberulent. Flowers rather small; calyx lobes lanceolate, 3–4 mm. long, minutely puberulent; corolla reflexed-rotate, dingy greenish yellow, the lobes 6–7 mm. long; gynostegium very shortly stipitate or essentially obsolete, pale greenish cream, the column broadly obconic, about 1 mm. long and 1.5 mm. broad, the hoods oblanceolate, about 5 mm. long, conspicuously narrowed to a narrowly laminate stipe from near the tip, the tip laminate and rather deeply emarginate, the horn wholly adnate to the sinus and more or less linguiform, enclosing the hood from above (rarely ascending), the anther head truncate-conic, about 1.5 mm. long and broad. Follicles erect on deflexed pedicels, more narrowly fusiform, rather narrowly attenuate, 6–9 cm. long, 1.0–1.5 cm. broad, minutely puberulent to glabrate; seeds broadly oval, about 8 mm. long, the pale tawny coma 2.5–3.5 cm. long.

Sandy prairies and dry plains, spreading to roadsides and railways. Southwestern Texas; northeastern Mexico. Blooming from April to August.

United States:

Texas: Bee, Callahan, Frio, Guadalupe, Hidalgo, Howard, Kleberg, La Salle, Live Oak, Mitchell, Nolan, Nueces, Schleicher, Uvalde, and Webb counties.

Mexico: Nuevo Leon: Obispado, Monterrey. Tamaulipas: Nuevo Laredo, San Miguel.

The typical extremes of *A. emoryi* are very easy to distinguish from typical *A. oenotheroides* by their floral structure, as the accompanying illustrations show; but rather frequent intergradations occur, possibly the result of at least occasional hybridization.

78. Asclepias **standleyi** Woodson, spec. nov.

Herbae perennes humiles. Caules ascendentes vel decumbentes validiuscules simplices ca. 1–4 dm. alti minute puberuli. Folia opposita longe petiolata lanceolata acuminata basi attenuata 5–10 cm. longa 1–3 cm. lata firme membranacea pallide viridia minute puberula; petiolis 1–2 cm. longis. Inflorescentiae plures vel multae pluriflorae sessiles vel subsessiles; pedicellis graciliusculis ca. 1 cm. longis dense puberulis. Flores parvi; calycis laciniis ovato-lanceolatis ca. 3 mm. longis minute puberulis; corolla reflexo-rotata sordide gilva, lobis 7–8 mm. longis; gynostegio subsessili sordide gilvo, columna subnulla, cucullis valde conduplicatis subquadratis ca. 4 mm. longis basi solidis apicem versus paullo laminatis, cornu per longitudinem adnato cristato, androecio ca. 2 mm. longo 3 mm. lato. Folliculi erecti e pedicellis deflexis latiscule fusiformes breviter apiculati ca. 7–8 cm. longi 1.5 cm. crassi laeves minutissime puberuli glabrati; seminibus late ovalibus ca. 8–9 mm. longis, coma alba ca. 2.5 cm. longa.—Holotypus: *J. G. Ortega 4548* in Herb. U. S. Nat. Mus. (Las Palmas, Sinaloa, Mexico, 1922).

MEXICO: SINALOA: Las Palmas, Fuerte.

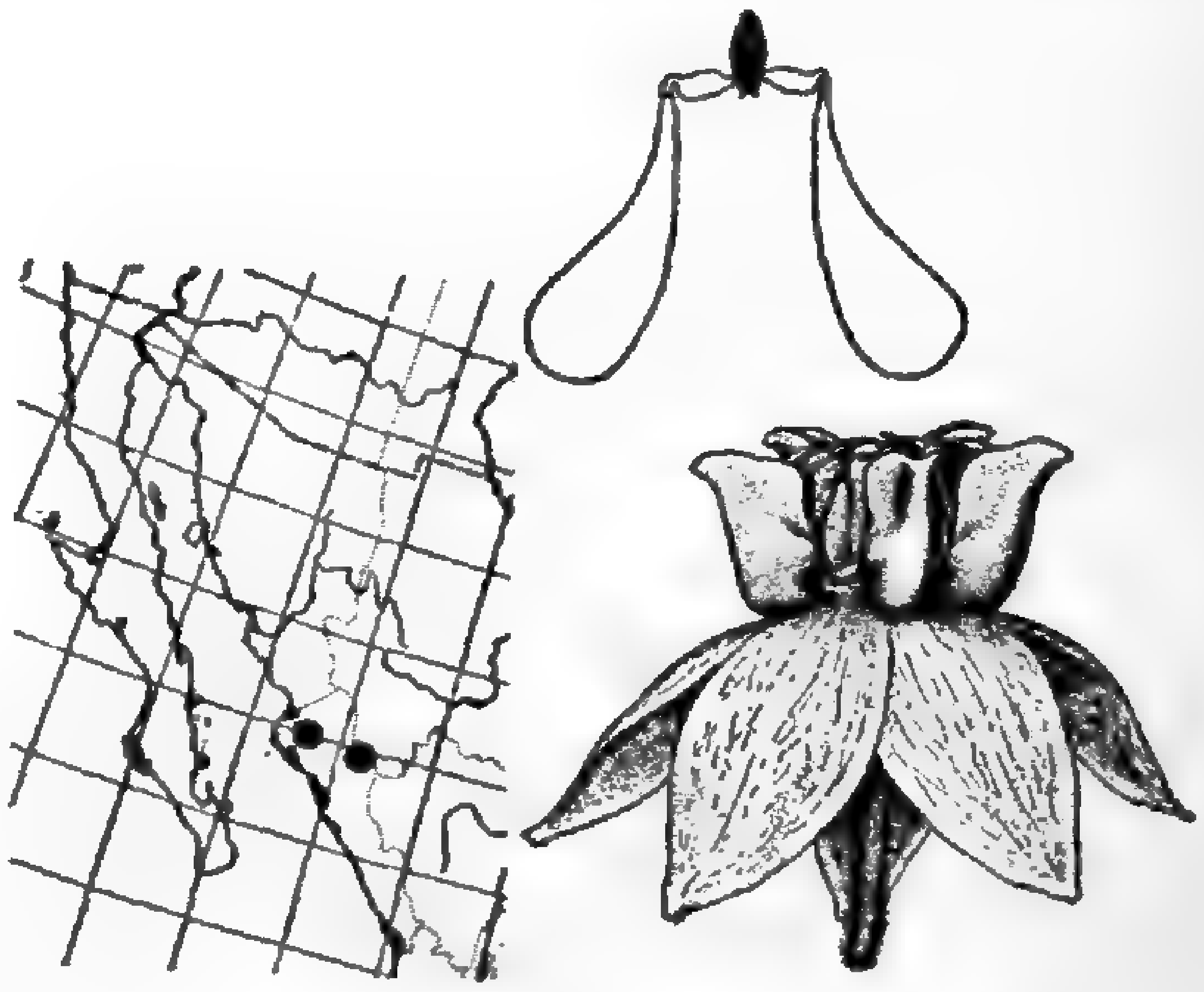

Fig. 84. *Asclepias standleyi* Woods.

This species also has been collected by Rose, Standley, & Russell (no. *13568* in Herb. U. S. Nat. Mus.) at Fuerte, Sinaloa. The hoods of *A. standleyi* are so short that, were it not for the characteristic aspect of the foliage, it might be mistaken for one of the ROSEAE of the subgenus ASCLEPIAS. Ortega reports the popular name as *hierba de la mula.*

SUBGENUS III. Anantherix (Nutt.) Woodson, stat. nov.

Anantherix Nutt. Gen. North Amer. Pl. 1:169. 1818; A Gray, in Proc. Amer. Acad. 12:66. 1877. [T.: *A. connivens* (Baldw.) Feay, ex Wood.]

79. Asclepias connivens Baldw. ex Ell. Sketch Bot. South Car. & Ga. 1:320. 1821, ex char.

Acerates connivens (Baldw.) Dcne. in DC. Prodr. 8:521. 1844.
Anantherix connivens (Baldw.) Fay, ex Wood, Classb. Bot. 584. 1861; A. Gray, in Proc. Amer. Acad. 12:66. 1877.

Herbaceous perennials. Stems rather stout, simple, 2–9 dm. tall, inconspicuously pilosulose to glabrate. Leaves opposite, sessile or subsessile, oval to oblong-elliptic below, becoming narrower and smaller above, apex acute to obtuse, base obtuse or rounded, 5–7 cm. long, 1.0–2.5 cm. broad, firmly membranaceous, somewhat

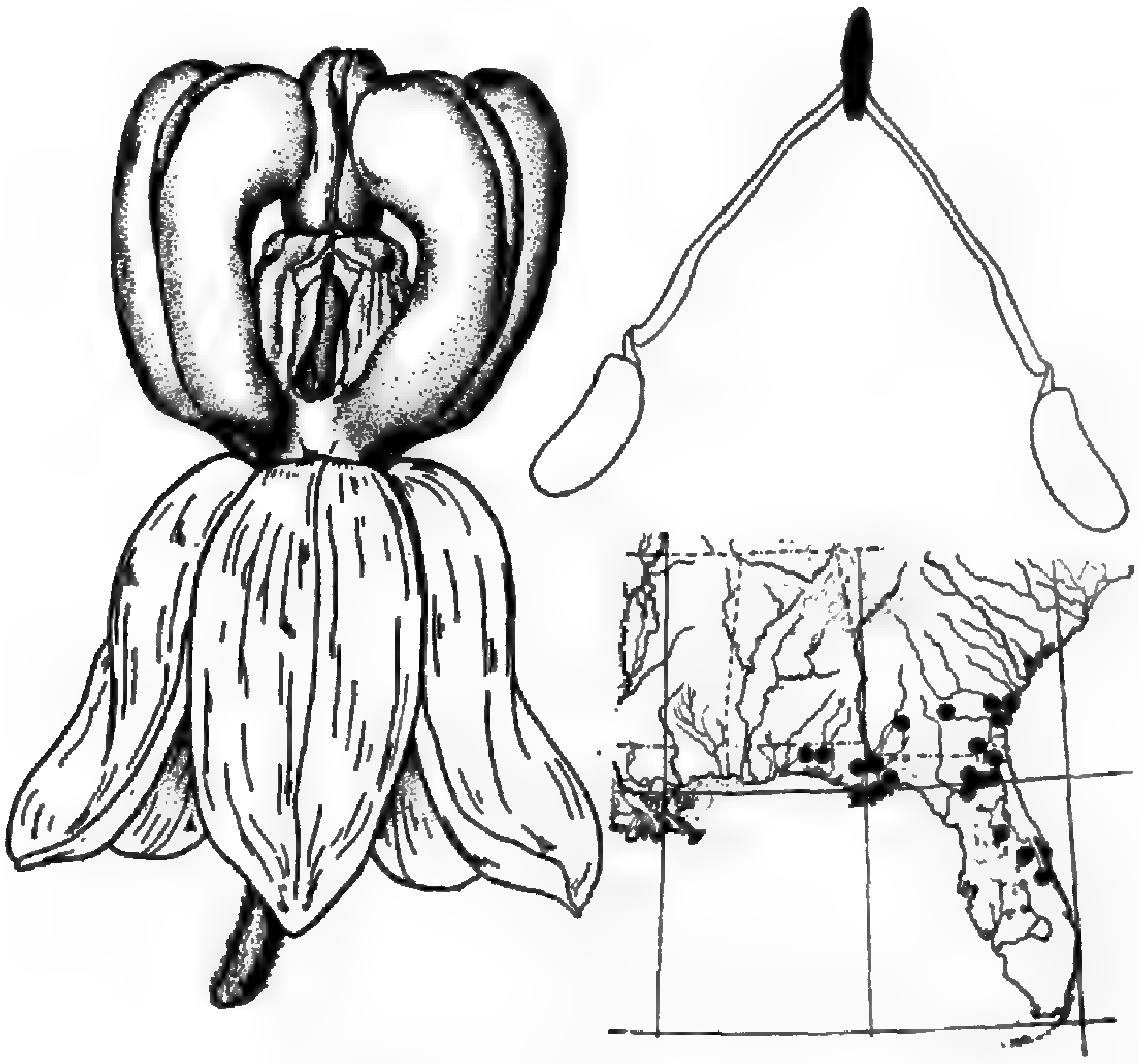

Fig. 85. *Asclepias connivens* Baldw.

glaucous, very inconspicuously pilosulose to glabrous. Inflorescences terminal and lateral at the uppermost nodes, few- to several-flowered, shortly pedunculate; peduncles 1.5–3.5 cm. long, relatively stout; pedicels more slender, 1.0–1.5 cm. long. Flowers large; calyx lobes lanceolate, 4–5 mm. long, glabrous; corolla reflexed-rotate, pale greenish yellow, the lobes 1.2–1.5 cm. long; gynostegium sessile or subsessile, the hoods involute-clavate, erect or ascending, scarcely laminate, 7–9 mm. long, with a low adnate crest within, pale greenish cream, the anther head truncate-conic, about 4 mm. long and 5 mm. broad. Follicles erect on deflexed pedicels, narrowly fusiform, gradually attenuate, 12–15 cm. long, smooth, essentially glabrous; seeds broadly oval, about 1 cm. long, the pale tawny coma about 4.5 cm. long.

Low pine woods and barrens, flatwoods, marshes. Northern Florida and southeastern Georgia. Blooming from June to August.

United States:

florida: Alachua, Bradford, Brevard, Calhoun, Clay, Duval, Franklin, Gadsden, Gulf, Lake, Orange, Wakulla, and Walton counties.

georgia: Charlton, Coffee, McIntosh, Wayne, and Worth counties.

One of the strangest species of *Asclepias*, rather resembling a terrestrial orchid. The flowers are very fragrant.

SUBGENUS IV. ASCLEPIODELLA (Small) Woodson, subgen. nov.

Asclepiodella Small, Man. Southeast. Fl. 1073. 1933. [T.: *A. feayi* (Chapm.) Small]

KEY TO THE SPECIES

a. Hoods with an internal horn or crest.
  b. Horns or crests compressed tangentially; hoods delicately petalaceous; follicles erect on erect pedicels, very narrowly fusiform; leaves opposite, filiform.
    c. Corolla white tinged with purple without, the lobes reflexed at anthesis; hoods with very conspicuous marginal auricles; column short but evident. South Carolina, southern Georgia and northern Florida ....80. *A. cinerea*
    cc. Corolla white, the lobes somewhat ascending at anthesis; hoods without marginal auricles; column obsolete. Peninsular Florida ....81. *A. feayi*
  bb. Horns compressed radially; hoods more or less fleshy and inflated; flowers reddish purple; follicles broadly fusiform.
    c. Plants usually rather stout, branching frequently; leaves normally opposite, linear-lanceolate, narrowly acuminate; inflorescences lateral, numerous, shortly but obviously pedunculate; follicles erect on deflexed pedicels. Southwestern Texas and southern New Mexico and Arizona; Coahuila to Sonora and southward to Guanajuato..82. *A. brachystephana*
    cc. Plants very small, branching only at the caudex; leaves approximate; inflorescences terminal or subterminal, rarely lateral, sessile.
      d. Leaves essentially isophyllous, broadly ovate; plants densely tomentulose; follicles erect on somewhat deflexed pedicels. Southern Utah and Nevada..................83. *A. ruthiae*
      dd. Leaves isophyllous, filiform; plants inconspicuously puberulent; follicles pendulous or weakly ascending. Southern Utah and northern Arizona............................84. *A. cutleri*
      ddd. Leaves heterophyllous, the lowermost ovate, sharply grading to linear-lanceolate above; plants inconspicuously puberulent; (follicles unknown). New Mexico and eastern Colorado ....85. *A. uncialis*
aa. Hoods without a horn or crest, more or less fleshy and inflated; plants glabrous; leaves ovate, cordate, sessile and deeply amplexicaul; corolla reddish purple; follicles erect on deflexed pedicels. Northern California and adjacent Oregon and Nevada............86. *A. cordifolia*

At one time (in Ann. Missouri Bot. Gard. 28:205. 1941) I tentatively placed these species in three subgenera: one for *A. cinerea* and *A. feayi,* one for *A. brachystephana* and its relatives, and one for *A. cordifolia.* Actually I still believe it might be more natural to maintain such a division here, perhaps as three series. But so few species are involved and the differences are so slight and of such little consequence in other subgenera that I do not feel enough inclined to do so, since the character which holds them together (the open saccate cucullate hood) is the chief consideration.

80. Asclepias cinerea Walt. Fl. Carol. 105. 1788, ex char.

Slender herbaceous perennials from rather fleshy fusiform rootstalks. Stems very slender, simple, 3–6 dm. tall, very inconspicuously puberulent in decurrent lines from the nodes. Leaves opposite, sessile, linear or filiform, 6–8 cm. long, 1–2 mm. broad, membranaceous, glabrous. Inflorescences terminal or subterminal and usually lateral from few to several of the uppermost nodes, few- to several-flowered, shortly pedunculate; peduncles 0.5–1.0 cm. long; pedicels slender, about 2 cm. long. Flowers mediocre; calyx lobes ovate-lanceolate, about 2 mm. long, purplish, essentially glabrous; corolla reflexed-rotate at anthesis, white more or less suffused with purple, the lobes about 6 mm. long; gynostegium very shortly stipitate, white, the column about 2 mm. long and 1 mm. broad, the hoods delicately petalaceous, deeply saccate, about 2–3 mm. long, with very conspicuous acuminate marginal auricles, the horn adnate to about the middle, acicular, somewhat longer than the hood, the anther head about 2 mm. long and 2.5 mm. broad. Follicles erect on

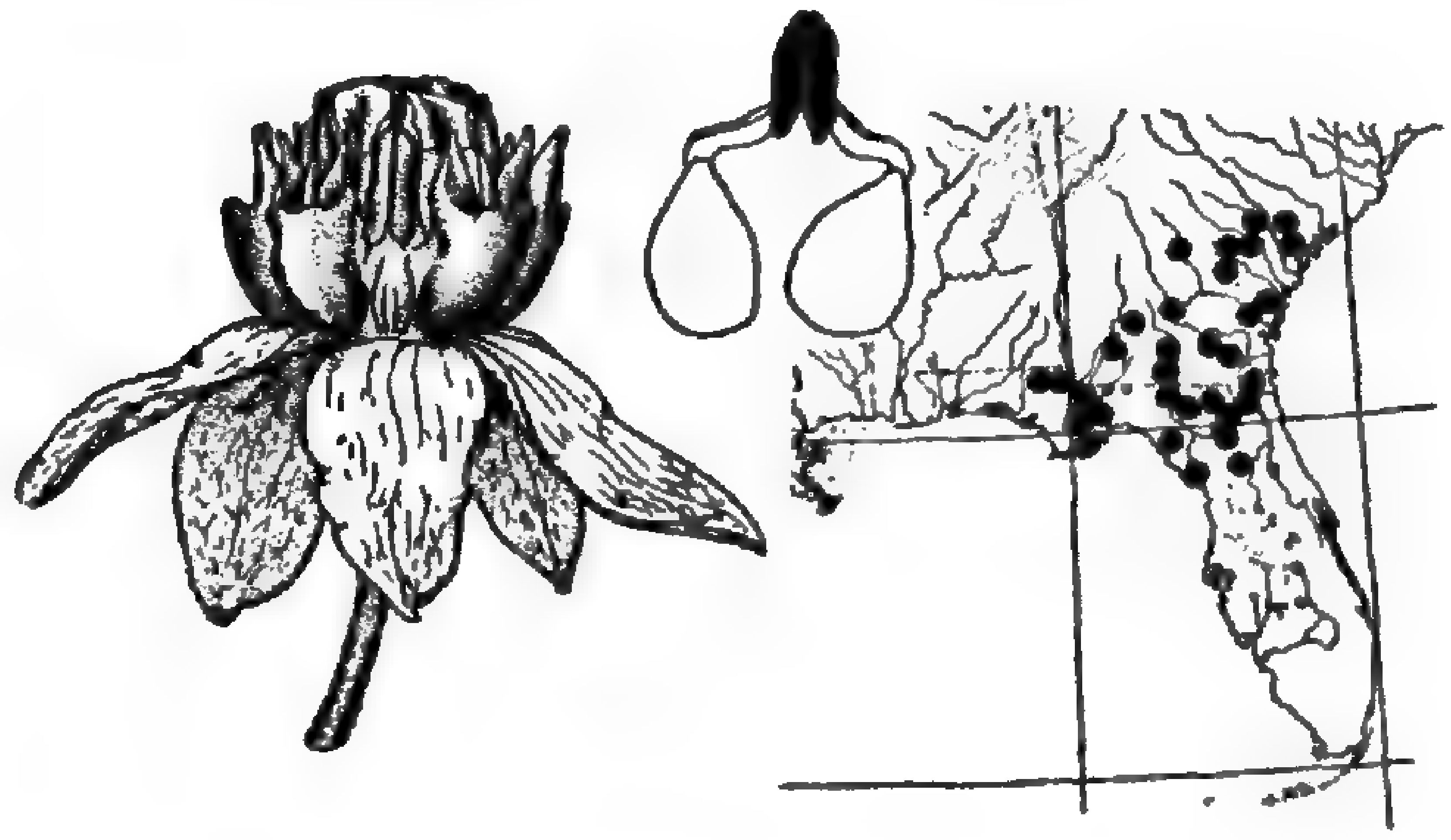

Fig. 86. *Asclepias cinerea* Walt.

erect pedicels, narrowly fusiform, gradually attenuate, 10–12 cm. long, about 5 mm. thick, smooth, glabrous; seeds broadly oval, about 8 mm. long, the white coma about 4 mm. long.

Pine woods and barrens, sandy ridges, spreading to meadows. Northern and central Florida, southern Georgia, southern South Carolina. Blooming from May to August.

United States:

florida: Alachua, Baker, Bradford, Calhoun, Columbia, Dixie, Duval, Franklin, Gadsden, Hamilton, Holmes, Jackson, Levy, Liberty, Marion, Nassau, Suwannee, and Union counties.

georgia: Ben Hill, Bullock, Candler, Charlton, Laurens, Lanier, Liberty, Lowndes, Mitchell, Screven, Toombs, Wayne, and Ware counties.

south carolina: Hampton and Jasper counties.

The prominent erect marginal auricles make it appear that the hoods contain three horns.

81. **Asclepias feayi** Chapm. ex A. Gray, in Proc. Amer. Acad. 12:72. 1877. [T.: *Chapman s. n.*, MO!]

Acerates feayi (Chapm.) Chapm. ex Coulter, Bot. Gaz. 3:12. 1878.
Asclepias simpsoni Chapm. Fl. South. U. S. ed. 2, 693. 1892. [T.: *Simpson s. n.*, MO!]
Asclepiodora feayi (Chapm.) Chapm. loc. cit. ed. 3, 349. 1897.
Asclepiodella feayi (Chapm.) Small, Man. Southeast. Fl. 1073. 1933.

Slender herbaceous perennials from slender fleshy rootstalks. Stems very slender, simple, 1.5–3.5 dm. tall, very inconspicuously puberulent in lines decurrent from the nodes. Leaves opposite, sessile, filiform, 7–9 cm. long, 1–2 mm. broad, delicately membranaceous, glabrous. Inflorescences terminal and solitary or also lateral from a few of the uppermost nodes, few-flowered, shortly pedunculate; peduncles slender, 0.5–1.5 cm. long; pedicels very slender, 1.0–1.5 cm. long. Flowers fairly large; calyx lobes ovate, 2–3 mm. long, purplish, glabrous; corolla rotate, white, the lobes about 1 cm. long; gynostegium sessile or subsessile, white, delicately petalaceous, the hoods broadly oval, about 3 mm. long, without marginal auricles, the horn reduced to a low wholly adnate crest, the anther head truncately conic, about 2 mm. long and 3 mm. broad. Follicles erect on erect pedicels, narrowly fusiform, gradually attenuate, 9–12 cm. long, about 5 mm. thick, smooth, glabrous; seeds oval, about 7 mm. long, the white coma about 3.5 cm. long.

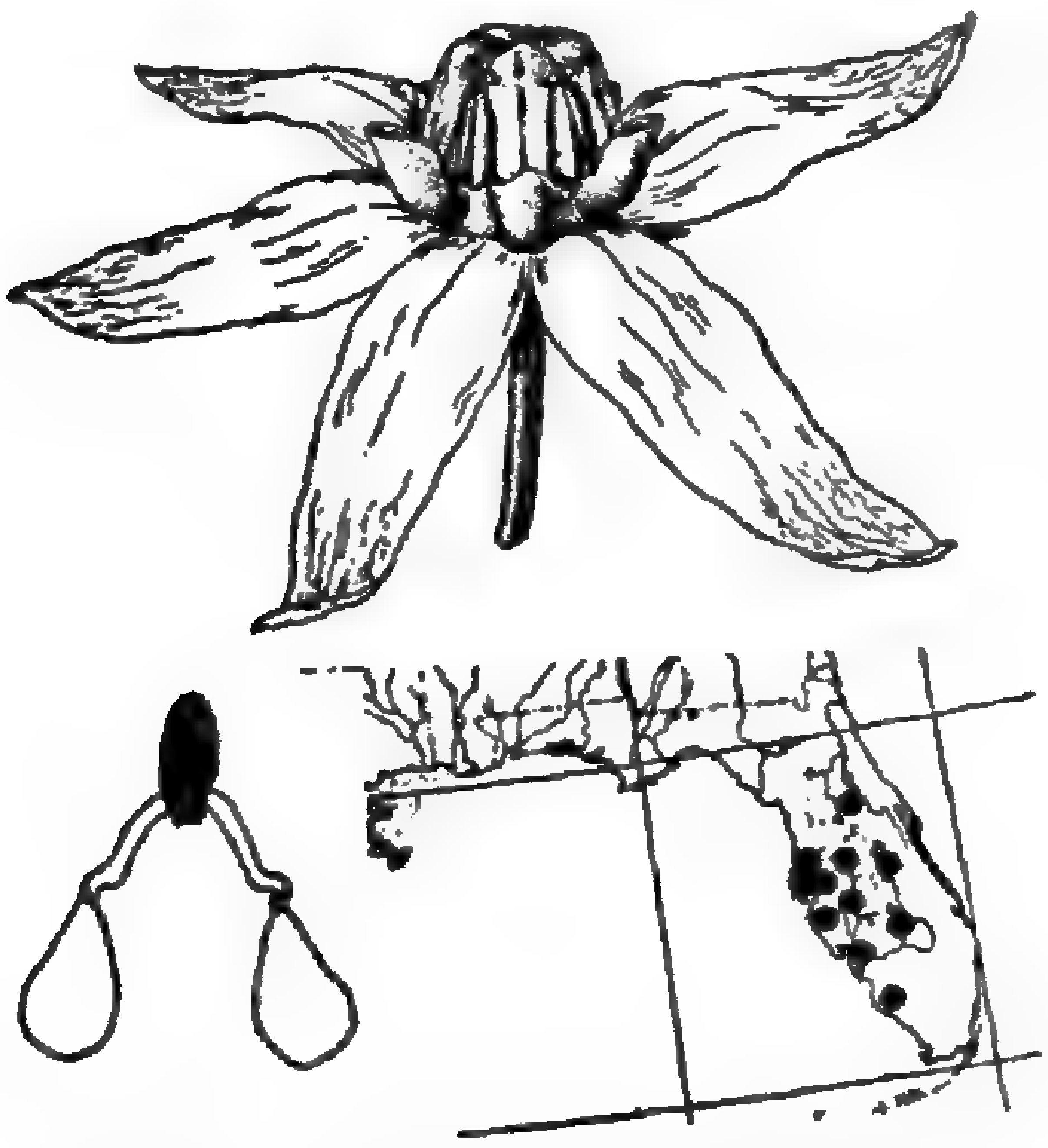

Fig. 87. *Asclepias feayi* Chapm.

Pine barrens, flatwoods, spreading to railways. Central Florida. Blooming from April to July.

United States:

florida: Collier, Hardee, Highlands, Hillsborough, Lake, Lee, Manatee, Osceola, Pasco, Pinellas, and Polk counties.

Asclepias simpsonii is still an enigma to me. The specimen collected by Dr. Simpson in the herbarium of the Missouri Botanical Garden is not very well preserved. Superficially, it is somewhat reminiscent of either *A. cinerea* or *A. feayi.* The floral structure is very difficult to examine, but seems to be somewhat intermediate as well, although somewhat suggestive of *A. verticillata!* It may be a natural hybrid, but has never been recollected.

82. **Asclepias brachystephana** Engelm. ex Torr. Bot. Mex. Bound. Surv. 163. 1859. [T.: *Wright 1692,* MO!]

Herbaceous perennials. Stems clustered from the rootstalk, rather slender, branching repeatedly toward the base, 1–4 dm. tall, minutely tomentulose when young, soon becoming glabrate. Leaves opposite, shortly petiolate, lanceolate to linear-lanceolate, narrowly acuminate, the base acute to obtuse, 6–12 cm. long, 0.5–1.2 cm. broad, firmly membranaceous, more or less conduplicate, minutely white-tomentulous when young, soon becoming glabrate; petioles 3–10 mm. long. Inflorescences lateral and solitary at the upper nodes, shortly pedunculate, several- to many-flowered; peduncles rather slender, 0.8–3.0 cm. long, conspicuously white-tomentulose; pedicels very slender, 1–2 cm. long, conspicuously white-tomentulose. Flowers rather small; calyx lobes ovate, about 2 mm. long, minutely puberulent; corolla reflexed-rotate, reddish purple or violet, the lobes 5–6 mm. long, the gynostegium sessile or subsessile, pale rose or cream, the hoods saccate, 1.5–2.0 mm. long, with very prominent marginal auricles somewhat longer than the broadly obtuse median lobe, the horn adnate about midway, linguiform, somewhat longer than the hood, the anther head truncately conic, about 2 mm. long and 3 mm. broad. Follicles erect on deflexed pedicels, broadly fusiform, rather gradually apiculate, 6–9 cm. long, 1–2 cm. thick, minutely puberulent to glabrate, longitudinally striate; seeds oval, about 7 mm. long, the pale tawny coma 2–3 cm. long.

Sandy and rocky plains, dry flats, gullies and stream banks, spreading to fields and roadsides, often eaten by livestock on overgrazed range. Western Texas and

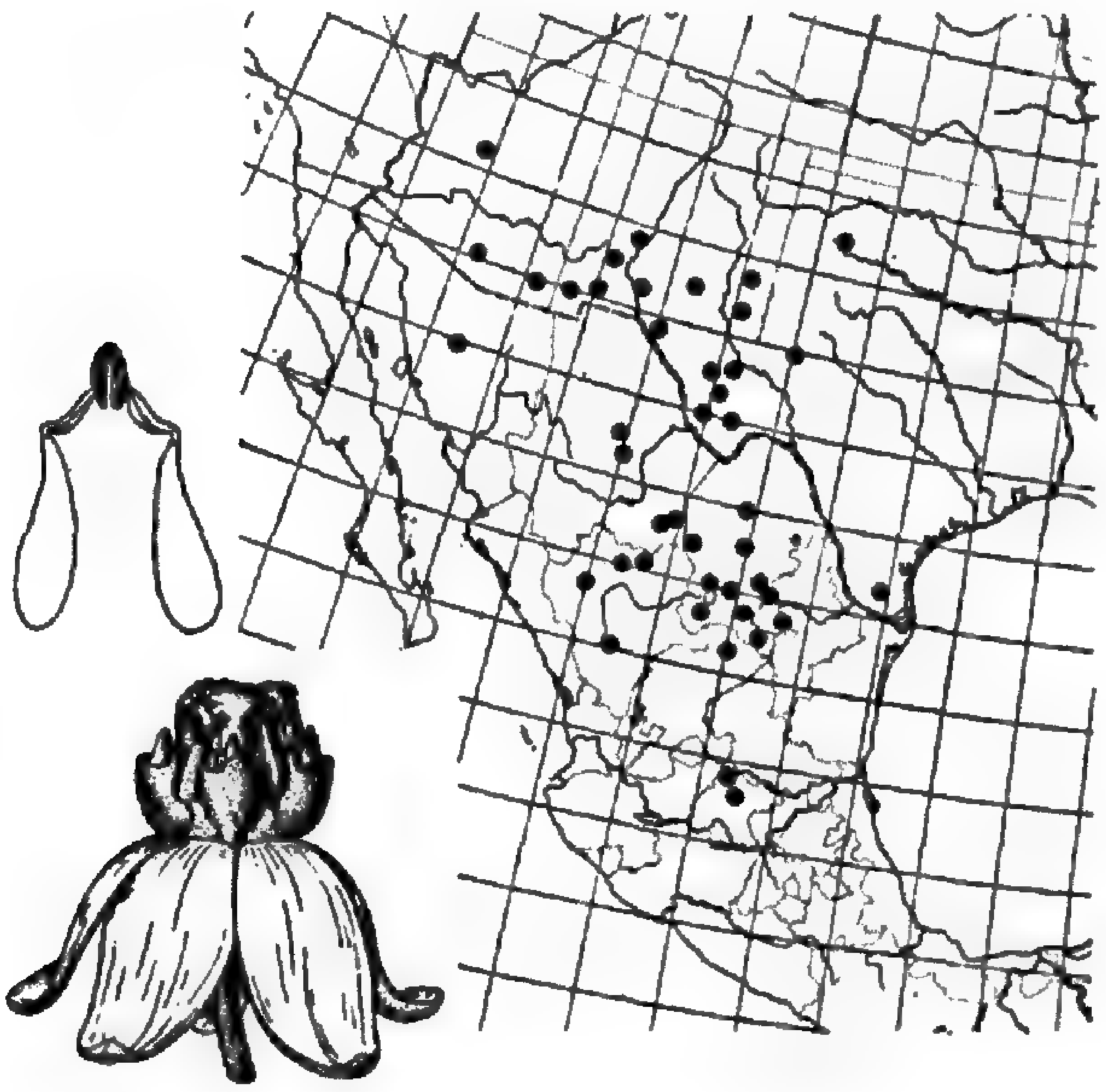

Fig. 88. *Asclepias brachystephana* Engelm.

southern New Mexico and Arizona; Coahuila to Sonora and southward to Guanajuato. Blooming from April to September.

UNITED STATES:

ARIZONA: Cochise, Pima, and Yavapai counties.

NEW MEXICO: Chaves, Dona Ana, Eddy, Hidalgo, Luna, Otero, Sierra, and Socorro counties.

TEXAS: Brewster, Culberson, El Paso, Hidalgo, Jeff Davis, Midland, Presidio, Randall, and Reeves counties.

MEXICO: CHIHUAHUA: Chihuahua, Escalón, Ciudad Jiménez, Santa Eulalia. COAHUILA: Saltillo, Parras, Sierra Mojada, Del Carmen, Torreón, Jimulco, Fraile, Movano, Múzquiz, Ramos Arispe, La Rosa, Hiplolito, Avalos. DURANGO: Tepehuanes, Durango, Inde, La Luz. GUANAJUATO: Guanajuato. SONORA: Llano. ZACATECAS: Cedros, Ojo Caliente.

83. ASCLEPIAS RUTHIAE Maguire, in Ann. Missouri Bot. Gard. 28:245, *fig. 1.* 1941. [T.: *Maguire 18310*, MO!]

Asclepias eastwoodiana Barneby, in Leafl. West. Bot. 4:210. 1945. [T.: *Ripley & Barneby 6196*, CAS!]

Small low herbaceous perennials. Stems ascending or somewhat decumbent, rather slender, simple or branching below ground, 6–9 cm. long, minutely tomentulose. Leaves opposite, petiolate, broadly ovate, apex shortly acuminate, base broadly obtuse or rounded, 1–5 cm. long, 1–3 cm. broad, glaucous, somewhat subsucculent, minutely and generally white-tomentulose, particularly the margins; petioles 2–10 mm. long. Inflorescences terminal or subterminal and occasionally lateral at the uppermost nodes, few-flowered, sessile; pedicels very slender, 1–2 cm. long, minutely tomentulose. Flowers small; calyx lobes ovate-lanceolate, about 3 mm. long, minutely tomentulose; corolla reflexed-rotate, pale violet, the lobes about 6 mm. long; gynostegium subsessile, pale rose-purple, the hoods saccate, truncate, about 1 mm. long, the horn linguiform, about as long as the hood, the anther head

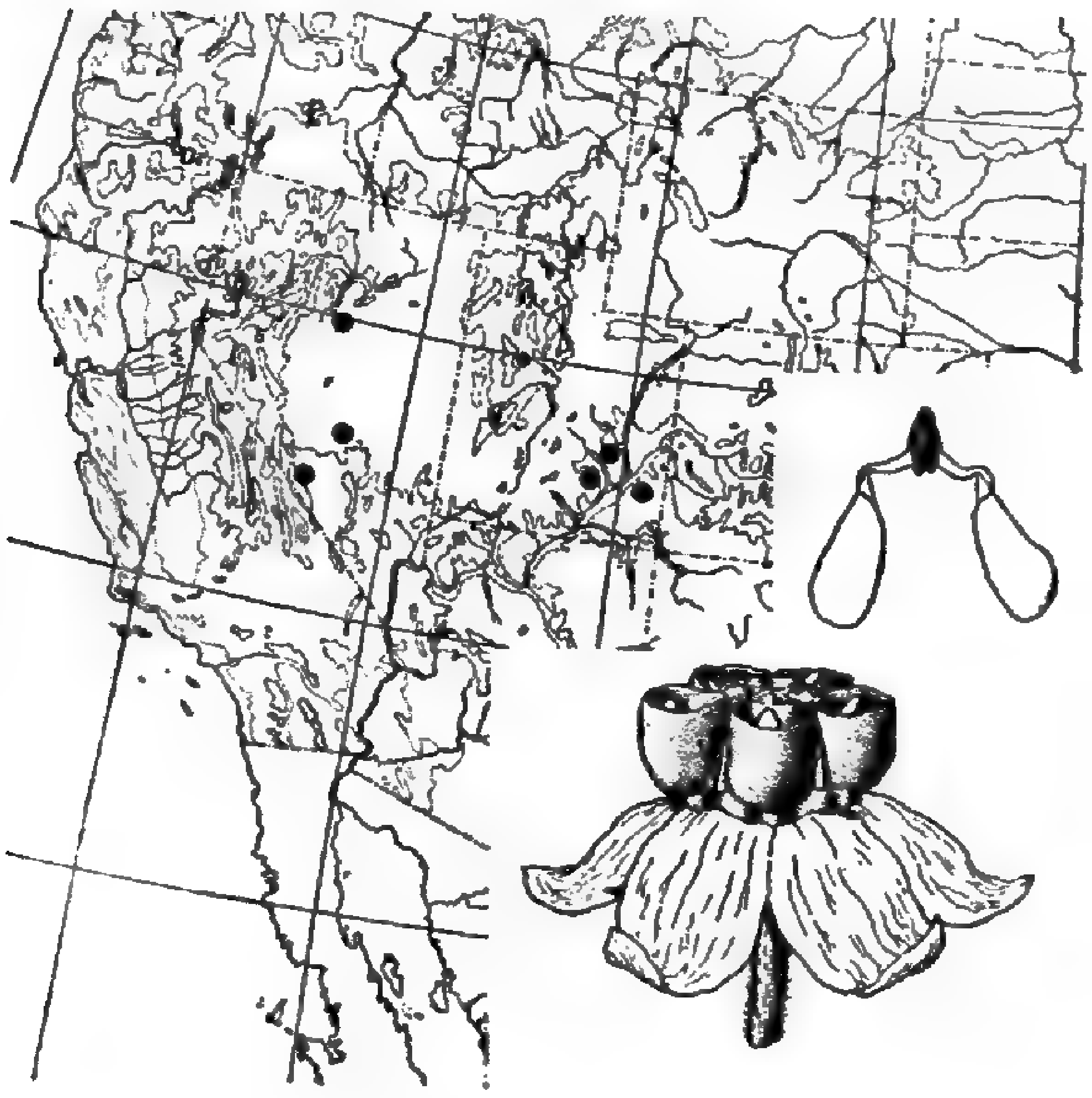

Fig. 89. *Asclepias ruthiae* Maguire

truncate-conic, about 1 mm. long and 1.5 mm. broad. Follicles erect on deflexed pedicels, broadly fusiform, abruptly apiculate, 3–4 cm. long, about 1.5 cm. thick, smooth, essentially glabrous; seeds broadly oval, about 1 cm. long, the white coma about 2 cm. long.

Low alkaline clay hills and rocky slopes of pinyon pine; red sand. Utah and central Nevada. Blooming from May to June.

United States:
nevada: Esmeralda, Lander, and Nye counties.
utah: Emery, San Juan, and Wayne counties.

84. **Asclepias cutleri** Woodson, in Ann. Missouri Bot. Gard. 26:263, *fig. 2.* 1939. [T.: *Cutler 2177,* MO!]

Small low herbaceous perennials. Stems very slender and weak, simple and branching only from the rootstalk, 6–13 cm. long, very inconspicuously puberulent. Leaves irregularly approximate, sessile, filiform, 3–8 cm. long, 1–2 mm. broad, lax, inconspicuously puberulent. Inflorescences terminal or subterminal, usually solitary, few-flowered, sessile; pedicels very slender, 5–10 mm. long, inconspicuously puberulent. Flowers small; calyx lobes lanceolate, about 3 mm. long; corolla reflexed-rotate, pale greenish rose, the lobes about 5 mm. long; gynostegium subsessile, pale rose, the hoods shortly saccate, about 1.5 mm. long, truncate but with prominent narrow marginal auricles, the horn linguiform, slightly longer

Fig. 90. *Asclepias cutleri* Woods.

than the hood, the anther head about 1 mm. long and 1.5 mm. broad. Follicles on pendulous to weakly ascending peduncles, narrowly fusiform, rather gradually attenuate, 4–5 cm. long, about 8 mm. thick, smooth, glabrous; seeds broadly oval, about 1 cm. long, the white coma about 1.5 cm. long.

Sand dunes and gravelly places. Southern Utah and adjacent Arizona. Blooming from April to June.

United States:
arizona: Apache County.
utah: Grand and San Juan counties.

85. Asclepias uncialis Greene, in Bot. Gaz. 5:64. 1880. [T.: *Greene s. n.*, MO!]

Small herbaceous perennials. Stems clustered from the rootstalk, ascending or somewhat decumbent, slender, simple, 1.5–4.0 cm. long, very inconspicuously puberulent. Leaves irregularly approximate, subsessile, heterophyllous, the lowermost ovate, abruptly grading to linear-lanceolate above, the apex acute to obtuse, the base obtuse to rounded, 1–2 cm. long, 2–7 mm. broad, very minutely puberulent. Inflorescences terminal or subterminal, few-flowered, sessile; pedicels very slender, 1.0–1.5 cm. long, minutely puberulent. Flowers small; calyx lobes ovate-lanceolate, about 2 mm. long, sparsely puberulent; corolla reflexed-rotate, purplish rose, the lobes about 4 mm. long; gynostegium sessile, pale rose, the hoods very shortly saccate, about 1.5 mm. long, truncate but with prominent acute marginal auricles, the horn inflated and linguiform, slightly longer than the hood, the anther head about 1 mm. long and 1.5 mm. broad. Follicles unknown.

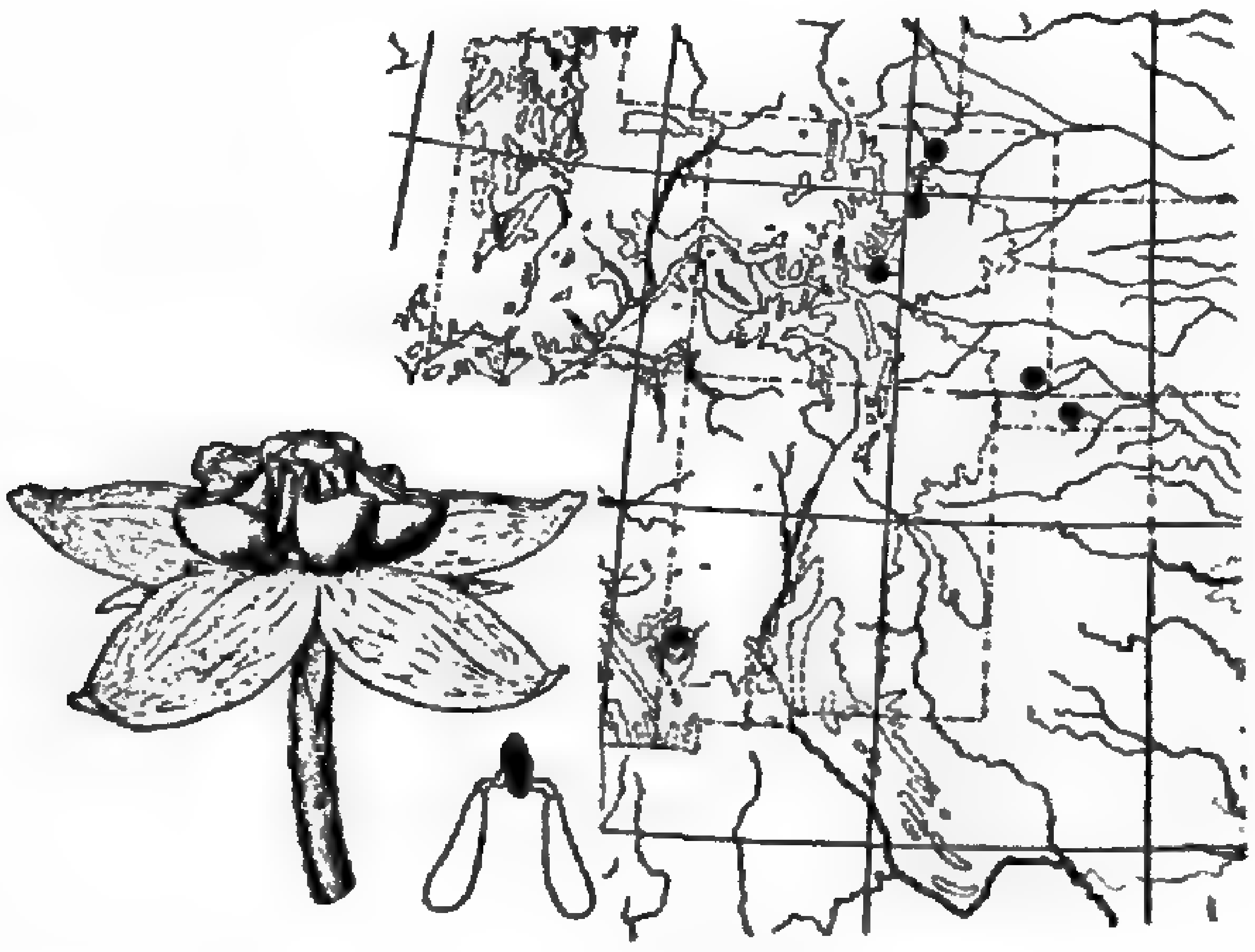

Fig. 91. *Asclepias uncialis* Greene

Sandy and rocky soil. Eastern Colorado and southwestern New Mexico. Flowering in May and June.

United States:
colorado: Baca, Denver, Fremont, Texas, and Weld counties.
new mexico: Grant County.

Asclepias ruthiae, A. cutleri, and *A. uncialis* are an odd little constellation of satellites about *A. brachystephana;* all greatly reduced in size and scattered in their arid distributions.

86. Asclepias cordifolia (Benth.) Jepson, Fl. West. Middle Calif. 384. 1901.

Acerates cordifolia Benth. Pl. Hartw. 323. 1849. [T.: *Hartweg 338*, MO photo!]
Asclepias acornutum Kellogg, in Proc. Calif. Acad. 1:54. 1855, ex char.
Acerates atropurpurea Kellogg, loc. cit. 68. 1855. [Based on *Asclepias acornutum* Kellogg]
Gomphocarpus cordifolius (Benth.) Benth. ex A. Gray, Bot. Calif. 1:477. 1876.

Herbaceous perennials. Stems rather stout, simple, 2–8 dm. tall, frequently flattened laterally, glaucous, glabrous. Leaves opposite, rarely ternate, sessile, ovate, apex abruptly acuminate to obtuse, base broadly cordate and amplexicaul, 7–12 cm. long, 5–10 cm. broad, glabrous, glaucous, firmly membranaceous or somewhat subsucculent. Inflorescences terminal or subterminal and usually solitary or clustered at the upper nodes, rather stoutly pedunculate, several- to many-flowered, wholly glabrous; peduncles 1–7 cm. long, rarely obsolete; pedicels very slender, 2–4 cm. long. Flowers rather small; calyx lobes ovate-lanceolate, about 3 mm. long, purplish, glabrous; corolla reflexed-rotate at anthesis, deep reddish purple or violet, the lobes 6–8 mm. long; gynostegium shortly stipitate, paler purple or violet, the column broadly obconic, about 1.5 mm. long and 2.5 mm. broad, the hoods saccate, about 3 mm. long, truncate but with very prominent, narrow marginal auricles, without internal horns. Follicles erect on deflexed pedicels, rather narrowly fusiform, gradually attenuate, 7–12 cm. long, about 1.5–2.0 cm. thick, glabrous; seeds broadly oval, about 8 mm. long, the white coma about 3.0–3.5 cm. long.

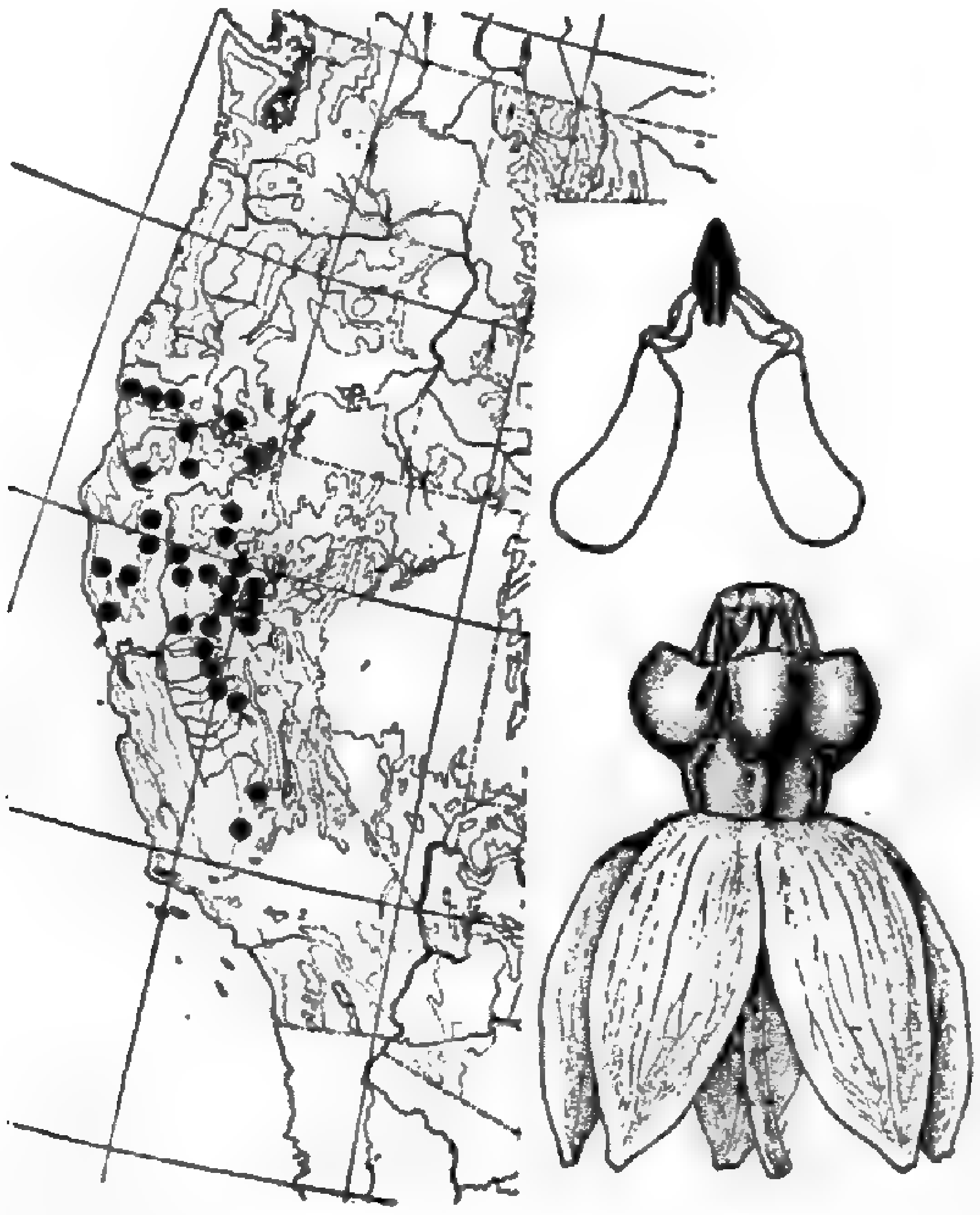

Fig. 92. *Asclepias cordifolia* (Benth.) Jepson

Talus slopes, gravelly places, upland woods and chaparral. Northern California and adjacent Oregon and Nevada. Blooming from May to July.

United States:

california: Amador, Butte, Calaveras, Eldorado, Glenn, Kern, Lake, Lassen, Mariposa, Modoc, Mendocino, Nevada, Placer, Plumas, Sacramento, Shasta, Sierra, Siskiyou, Sonoma, Sutter, Tulare, Tuolumne, Trinity, and Yuba counties.

NEVADA: Douglas, Ormsby, and Washoe counties.

OREGON: Curry, Jackson, Josephine, and Lake counties.

SUBGENUS V. ACERATES (Ell.) Woodson, stat. nov.

Acerates Ell. Sketch Bot. South Car. & Ga. 1:316. 1821. [T.: *A. longifolia* (Michx.) Ell.]

KEY TO THE SPECIES

a. Corona with a short but definite column, the hoods much shorter than the anther head; anther wings conspicuously notched; pollinium sacs rather abruptly constricted to the translator.
  b. Leaves ovate to ovate-elliptic; flowers reddish purple; anther head about as long as broad, the wings salient at the base. Oaxaca ..... 87. *A. vinosa*
  bb. Leaves linear; flowers pale green frequently tinged with livid purple; anther head somewhat broader than long, the wings salient at the middle.
    c. Inflorescences lateral, numerous, dense and nearly spherical, the flowers very slightly tinted with purple; plants relatively stout. Ohio and Tennessee westward to southern Minnesota and Oklahoma ..... 88. *A. hirtella*
    cc. Inflorescences both terminal and lateral, the lateral rather few, rather lax and hemispherical, the flowers rather liberally tinted with purple; plants rather slender. Coastal Plain: Delaware to Florida and Louisiana ..... 89. *A. longifolia*
aa. Corona sessile, the hoods nearly as long as the anther head; anther wings not notched; pollinium sacs gradually attenuate to the translator.
  b. Inflorescences usually lateral, numerous; anther wings salient above the middle; pollinium sacs extremely narrow and attenuate. Southern Ontario and Manitoba; Connecticut to Georgia and westward to eastern Montana and Arizona; northern Coahuila ..... 90. *A. viridiflora*
  bb. Inflorescences terminal and solitary; anther wings salient below the middle; pollinium sacs moderately narrow and attenuate. Southern Wisconsin and northern Illinois westward to North Dakota and Kansas ..... 91. *A. nuttalliana*

87. ASCLEPIAS vinosa (Fourn.) Woodson, comb. nov.

Acerates vinosa Fourn. in Ann. Sci. Nat. Bot. Ser. VI, 14:387. 1882. [T.: *Ghiesbreght 35*, P!]

Low herbaceous perennials. Stems rather slender, simple or branching from the caudex, about 1.5 dm. long, inconspicuously puberulent. Leaves opposite, long-petiolate, ovate to ovate-elliptic, apex obtuse to acute, base obtuse to broadly rounded, 4–6 cm. long, 1.5–3.0 cm. broad, firmly membranaceous, inconspicuously puberulent below, glabrate above; petioles 1.0–1.5 cm. long. Inflorescences terminal, solitary, several- to rather many-flowered, shortly pedunculate; peduncle about 1.5 cm. long, minutely puberulent; pedicels slender, about 1 cm. long, minutely puberulent. Flowers rather small; calyx lobes ovate-lanceolate, about 3 mm. long, minutely and rather sparsely puberulent; corolla reflexed-rotate, dull reddish, the lobes about 6 mm. long; gynostegium very shortly but definitely

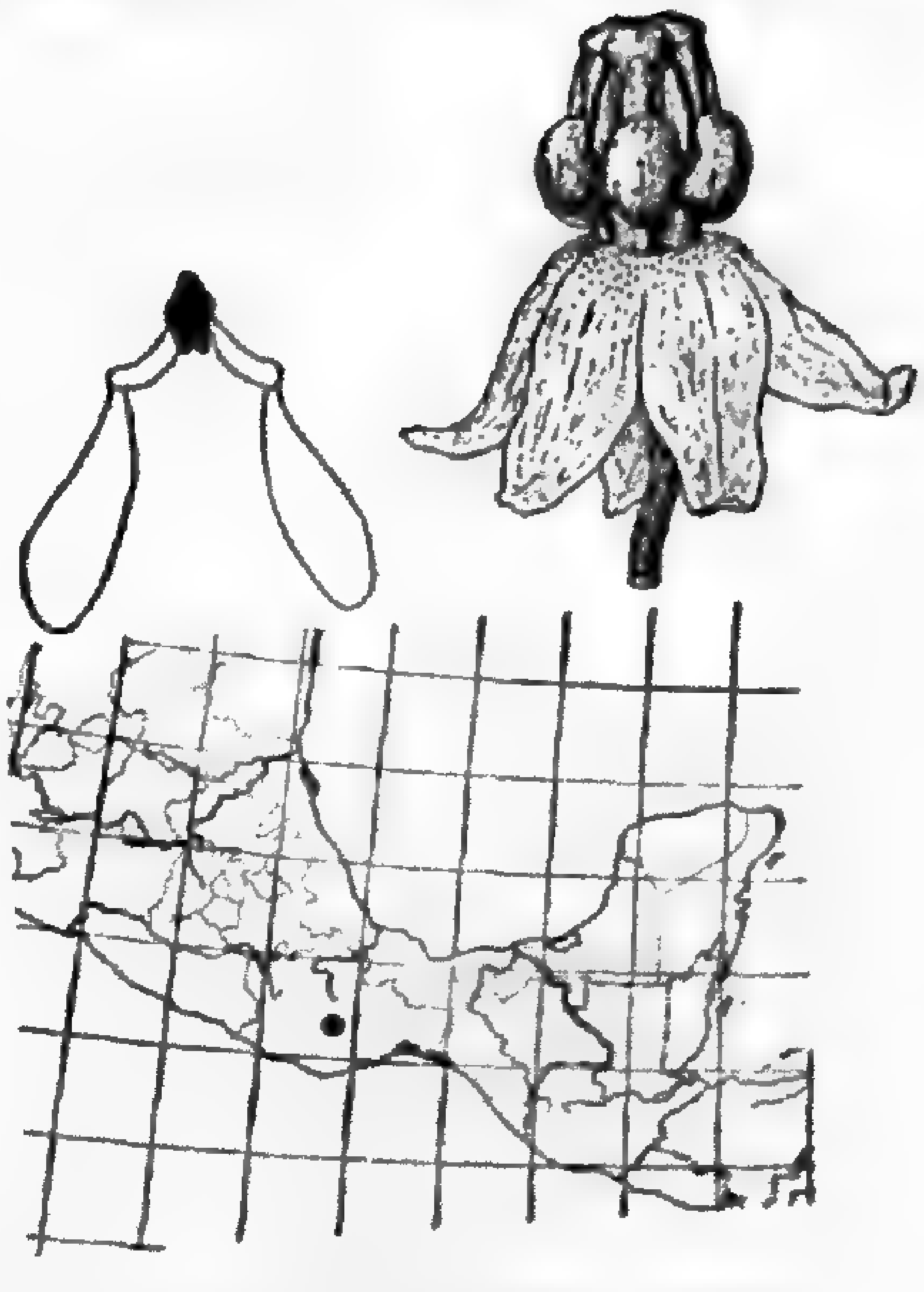

Fig. 93. *Asclepias vinosa* (Fourn.) Woods.

stipitate, reddish, the column very broadly obconic, about 1 mm. long and 1.5 mm. broad, the hoods saccate, ovoid, about 1.5 mm. long, much lower than the anther head, without a horn, the anther head truncate-conic, about 2 mm. long and 3 mm. broad. Follicles unknown.

Pine forests. Oaxaca. Blooming in June.

Mexico: oaxaca: locality unknown.

At first glance the type specimen, which is the sole representative of the species, resembles *A. viridiflora.* But the floral structure, especially the very short hoods, is quite unlike any other species.

88. Asclepias hirtella (Pennell) Woodson, in Ann. Missouri Bot. Gard. 28:207. 1941.

Oligoron longifolium var. *hirsutum* Raf. in New Fl. North Amer. 4:60. 1838, ex char.
Acerates hirtella Pennell, in Bull. Torrey Bot. Club 46:184. 1919. [T.: *Pennell 5372*, NY!]

Herbaceous perennials. Stems rather stout, simple or occasionally branching from the base, 3–10 dm. tall, rather densely pilosulose. Leaves irregularly approximate, shortly petiolate to subsessile, linear-lanceolate, apex gradually acuminate, base narrowly acute, 7–16 cm. long, 0.6–1.5 cm. broad, firmly membranaceous, minutely pilosulose particularly beneath; petioles obsolete to about 8 mm. long. Inflorescences lateral and solitary at several to many of the upper nodes, shortly pedunculate, many-flowered, very dense and hemispherical; peduncles nearly obsolete to 4 cm. long, densely pilosulose; pedicels rather slender, 1.5–2.0 cm. long, densely tomentulose. Flowers rather small; calyx lobes ovate, 2–3 mm. long,

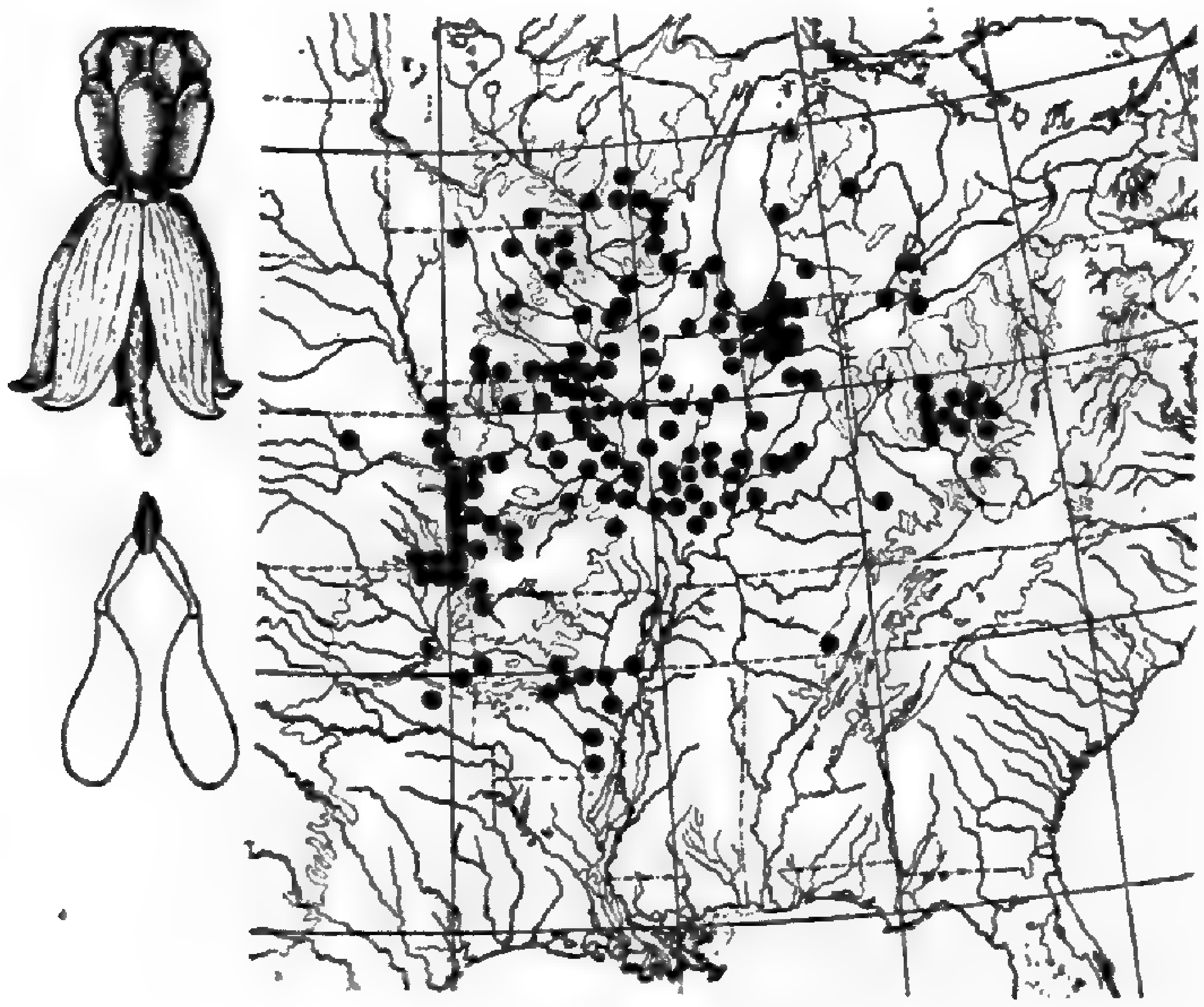

Fig. 94. *Asclepias hirtella* (Pennell) Woods.

densely and minutely pilosulose; corolla reflexed-rotate, pale green very slightly tinted with purple without, the lobes about 4–5 mm. long, gynostegium pale green, very shortly but definitely stipitate, the column about 1.5 mm. long and 1 mm. broad, the hoods deeply saccate, oblong-ovoid, about 2 mm. long, much lower than the anther head, the anther head about 1.5 mm. long and broad. Follicles erect on deflexed pedicels, rather narrowly fusiform, long-attenuate, 6–15 cm. long, about 1–2 cm. thick, very densely pilose-puberulent; seeds broadly oval, about 9 cm. long, the pale tawny coma 3.5–4.0 cm. long.

Prairies, open woods, sandy or clay soil, spreading to fields, roadsides, railways, and waste places. Southern Ontario; western West Virginia and Tennessee westward to southern Minnesota and Oklahoma. Blooming from May to September.

CANADA: ONTARIO: Essex County.

UNITED STATES:

ARKANSAS: Arkansas, Ashley, Benton, Drew, Faulkner, Izard, Lonoke, Prairie, Pulaski, Saline, Sebastian, and Saint Francis counties.

INDIANA: Cass, Clinton, Daviess, Elkhart, Fulton, Jasper, Lake, La Porte, Lawrence, Martin, Newton, Porter, Pulaski, St. Joseph, Starke, Tipton, Vandenburgh, Vigo, and White counties.

IOWA: Appanoose, Black Hawk, Cerro Gordo, Chickasaw, Clinton, Davis, Decatur, Emmet, Fayette, Henry, Johnson, Lee, Ringgold, Scott, Story, Union, Van Buren, and Winneshiek counties.

KANSAS: Atchison, Bourbon, Cloud, Crawford, Cherokee, Johnson, Labette, Leavenworth, Linn, Miami, and Montgomery counties.

KENTUCKY: Madison County.

ILLINOIS: Adams, Cass, Champaign, Christian, Clay, Clinton, Cook, Crawford, Cumberland, Effingham, Fayette, Franklin, Greene, Hancock, Henderson, Iroquois, Jackson, Jefferson, Jo Daviess, Kankakee, La Salle, Lawrence, McHenry, Macoupin, Marion, Peoria, Piatt, Perry, Randolph, Richland, Schuyler, Stark, Wabash, Washington, Webster, Will, Williamson, and Winnebago counties.

MICHIGAN: Bay, Berrien, Kalamazoo, and Muskegon counties.

MINNESOTA: Mower County.

MISSOURI: Adair, Boone, Cass, Cedar, Clark, Franklin, Green, Grundy, Holt, Iron, Jackson, Jasper, Lafayette, Lincoln, McDonald, Maries, Montgomery, Marion, Pike, Polk, Ralls, Randolph, St. Louis, Scotland, and Vernon counties.

OHIO: Athens, Erie, Gallia, Jackson, Lucas, Meigs, Pickaway, Pike, Ross, Scioto, and Vinton counties.

OKLAHOMA: Craig, LeFlore, Muskogee, Nowata, Ottawa, and Pushmataha counties.

TENNESSEE: Franklin County.

WEST VIRGINIA: Jackson, Lincoln, and Wood counties.

WISCONSIN: Adams, Columbia, Dane, Juneau, Kenosha, La Crosse, Marquette, Rock, and Wood counties.

Asclepias hirtella and *A. longifolia* are so closely related that they might better be treated as subspecies. The ranges are quite distinct, however, and the plants look so different in the field that I must maintain them as species in spite of the very similar floral structures.

89. ASCLEPIAS LONGIFOLIA Michx. Fl. Bor.-Amer. 1:116. 1803, ex char.

Asclepias incarnata Walt. Fl. Carol. 106. 1788, non L., ex char.
Anthanotis procumbens Raf. Fl. Ludov. 52. 1817, ex char.
Acerates longifolia (Michx.) Ell. Sketch Bot. S. Carol. & Ga. 1:317. 1821.

Gomphocarpus longifolius (Michx.) Spreng. Syst. 1:849. 1825.
Polyotus longifolius (Michx.) Nutt. in Trans. Amer. Phil. Soc. n. s. 5:200. 1837.
Oligoron longifolium (Michx.) Raf. New Fl. North Amer. 4:60. 1838.
Acerates incarnata (Walt.) Dcne. in DC. Prodr. 8:523. 1844.
Acerates floridana (Lam.) Hitchc. in Trans. Acad. Sci. St. Louis 5:508. 1891, as to specimens cited, in part, not as to type specimen.
Acerates delticola Small, Man. Southeast. Fl. 1067. 1933. [T.: *Ingalls s. n.*, NY!]

Herbaceous perennials from a stout rather tuberous rootstalk. Stems rather slender, simple, 2–7 dm. tall, minutely pilosulose. Leaves irregularly approximate, sessile or subsessile, linear-lanceolate, gradually acuminate, the base attenuate, 6–18 cm. long, 2–10 mm. broad, minutely pilosulose to glabrate. Inflorescences terminal and solitary and lateral from few of the uppermost nodes, several- to rather many-flowered, rather lax and hemispherical, pedunculate; peduncles slender, 2–6 cm. long, rarely obsolete, minutely pilosulose; pedicels very slender, 1.5–2.0 cm. long, minutely pilosulose. Flowers small; calyx lobes lanceolate, about 2 mm. long, minutely pilosulose; corolla reflexed-rotate, pale greenish white liberally tinted with purple, particularly without, the lobes about 5 mm. long; gynostegium shortly but definitely stipitate, greenish white tinted with purple below, the column about 1.5 mm. long and 1 mm. broad, the hoods deeply saccate, obovoid, about 2 mm. long, without a horn, much lower than the anther head, the anther head about 1.5 mm. long and broad. Follicles erect on deflexed pedicels, narrowly fusiform, long-attenuate, minutely pilosulose, 8–12 cm. long, about 1 cm. thick, seeds rather broadly oval, about 1 cm. long, the white coma about 3.5 cm. long.

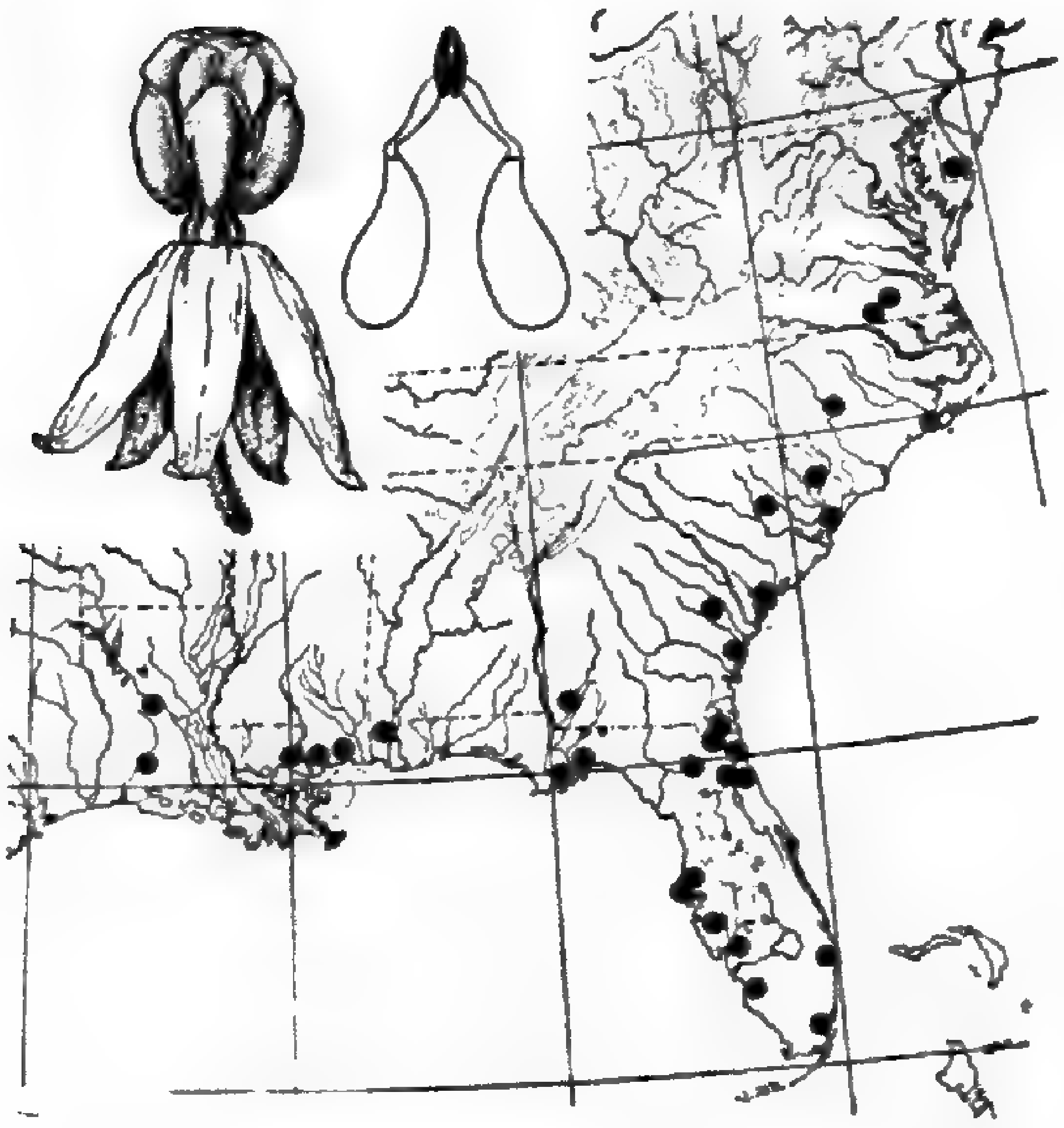

Fig. 95. *Asclepias longifolia* Michx.

Flatwoods, swamps, and low pinelands. Coastal Plain: Delaware to Florida and westward to Louisiana. Blooming from April to July.

United States:
alabama: Mobile County.
delaware: Sussex County.
florida: Alachua, Collier, Dade, Duval, Flagler, Franklin, Lee, Manatee, Nassau, Pasco, Pinellas, Putnam, St. Johns, and Wakulla counties.
georgia: McIntosh, Miller, and Sumter counties.
louisiana: Jefferson Davis, Rapides, and St. Tammany parishes.
mississippi: Hancock and Harrison counties.
north carolina: Carteret and Johnston counties.
south carolina: Beaufort, Georgetown, Marion, and Sumter counties.
virginia: Greensville and Sussex counties.

90. ASCLEPIAS VIRIDIFLORA Raf. Med. Repos. N. Y. 5:360. 1808, ex char.

Asclepias lanceolata Ives, Amer. Jour. Sci. 1:252. 1819, non Walt, ex char.

Asclepias viridiflora β lanceolata (Ives) Torr. Fl. North. & Mid. U. S. 1:284. 1824, ex char.

Gomphocarpus viridiflorus (Raf.) Spreng. Syst. 1:849. 1825.

Acerates viridiflora (Raf.) Pursh ex Eaton, Man. ed. 5, 90. 1829.

Polyotus heterophyllus Nutt. in Trans. Amer. Phil. Soc. n. s. 5:199. 1837, ex char. [T.: *Nuttall s. n.*]

Otanema lanceolata (Ives) Raf. New Fl. North Amer. 4:61. 1838.

Otanema latifolia Raf. New Fl. North Amer. 4:61. 1838, ex char.

Otanema ovata Raf. loc. cit. 1838, ex char.

Asclepias nutans Muhl. ex Steud. Nom. ed. 2, 1:146. 1841, ex char.

Acerates lanceolata Ell. ex Steud. loc. cit. 12. 1841, ex char.

Acerates viridiflora var. *lanceolata* (Ives) A. Gray, Syn. Fl. N. Amer. 2^1:99. 1878.

Acerates viridiflora var. *linearis* A. Gray, loc. cit. 1878, ex char.

Acerates viridiflora ivesii Britton, in Mem. Torrey Bot. Club 5:265. 1894. [Based on *Asclepias lanceolata* Ives.]

Asclepias ivesii (Britton) Woot. & Standl. in Contr. U. S. Nat. Herb. 19:509. 1905.

Acerates linearis (A. Gray) Lunell, in Amer. Midl. Nat. 4:509. 1916.

Asclepias viridiflora var. *linearis* (A. Gray) Fern. in Rhodora 48:208. 1946.

Herbaceous perennials. Stems usually rather stout, simple, rarely branching at the base, 1.5–9.0 dm. tall, inconspicuously puberulent to glabrate. Leaves opposite to irregularly approximate, shortly petiolate to subsessile, extremely variable, suborbicular to linear, 4–13 cm. long, 1–6 cm. broad, firmly membranaceous, incon-

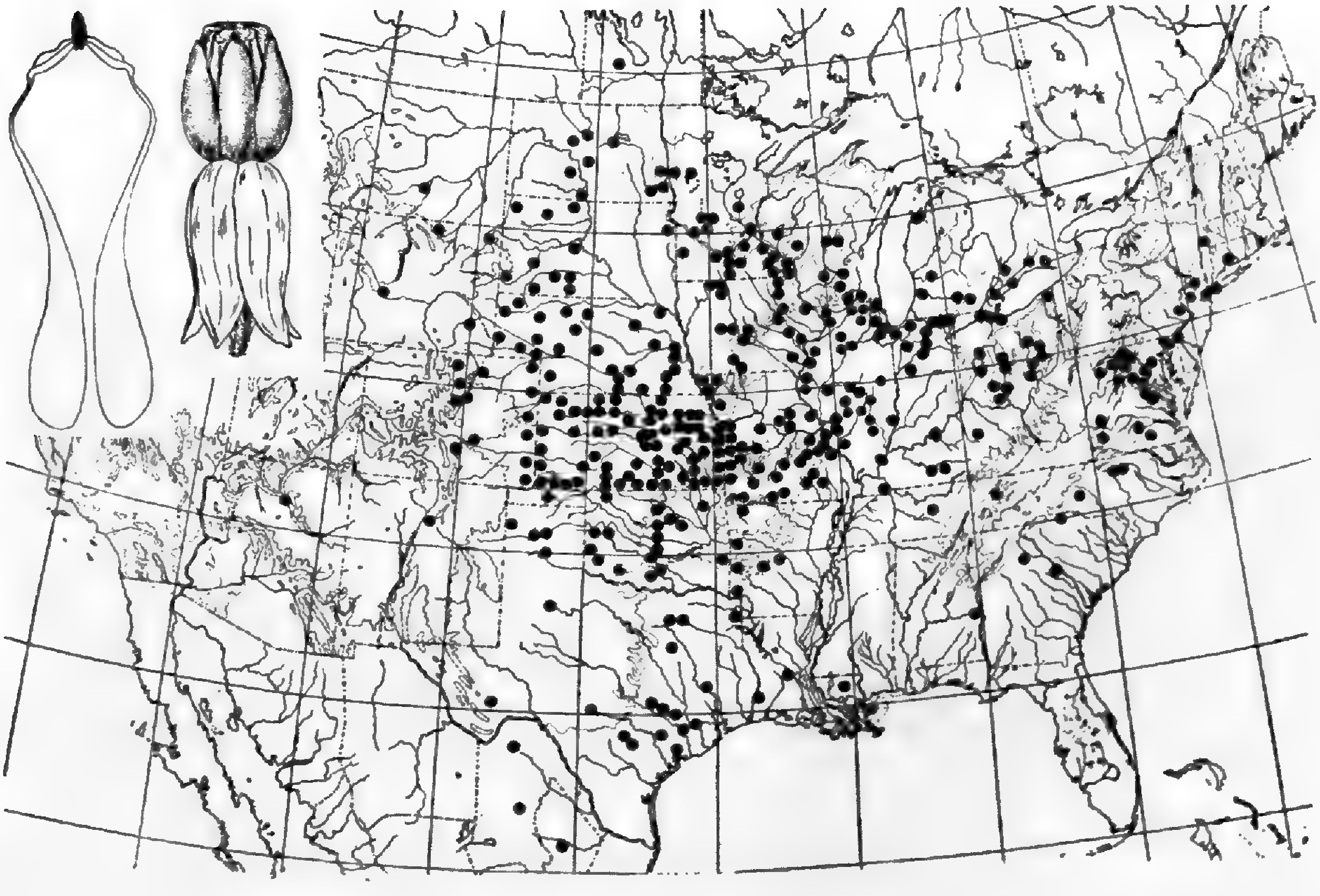

Fig. 96. *Asclepias viridiflora* Raf.

spicuously puberulent to glabrate; petioles obsolete to 1 cm. long. Inflorescences subterminal and solitary and usually lateral at few to many of the upper nodes, usually rather many-flowered, crowded and hemispherical, usually rather shortly pedunculate, puberulent; peduncles obsolete to 1.5 cm. long, rather stout; pedicels more slender, 1–2 cm. long. Flowers moderately large; calyx lobes ovate-lanceolate, 3–4 mm. long, minutely puberulent; corolla reflexed-rotate, pale green, the lobes 6–7 mm. long; gynostegium sessile, pale green, the hoods deeply saccate, oblongoid, 4–5 mm. long, nearly equalling the anther head, the anther head 3–4 mm. long. Follicles erect on deflexed pedicels, narrowly fusiform, long-attenuate, 7–15 cm. long, 1.5–2.0 cm. thick, finely puberulent to glabrate; seeds oval, 6–7 mm. long, the pale tawny coma 3–5 cm. long.

Glades, prairies, plains, and rocky or sandy hillsides, spreading to old fields and roadsides. Southern Ontario and Manitoba; Connecticut to Georgia and westward to Montana and Arizona; Coahuila. Blooming from April to August.

CANADA: MANITOBA: Norfolk County. ONTARIO: Essex, Kent, Lambton, Norfolk, and Oxford counties.

UNITED STATES:

ALABAMA: Lee County.

ARIZONA: Coconino County.

ARKANSAS: Carroll, Garland, Little River, Pope, Pulaski, and Sebastian counties.

COLORADO: Baca, Boulder, Cheyenne, Denver, El Paso, Fremont, Jefferson, Kit Carson, Larimer, Prowers, Sedgwick, Weld, and Yuma counties.

CONNECTICUT: New Haven County.

DELAWARE: New Castle County.

GEORGIA: Clarke and Richmond counties.

ILLINOIS: Adams, Boone, Carroll, Cass, Champaign, Christian, Coles, Cook, Du Page, Effingham, Hancock, Hardin, Henderson, Jo Daviess, Lake, Lee, McHenry, Macon, Macoupin, Madison, Marshall, Mason, Monroe, Peoria, Richland, St. Clair, Stark, Whiteside, and Will counties.

INDIANA: Cass, Elkhart, Fulton, Harrison, Jasper, La Grange, Lake, La Porte, Marshall, Steuben, and Tippecanoe counties.

IOWA: Benton, Black Hawk, Buchanan, Carroll, Decatur, Dickinson, Dubuque, Emmet, Fayette, Greene, Henry, Johnson, Muscatine, Palo Alto, Polk, Story, Union, and Winneshiek counties.

KANSAS: Anderson, Barber, Butler, Chase, Cherokee, Cheyenne, Clay, Cloud, Comanche, Cowley, Crawford, Decatur, Dickinson, Edwards, Elk, Ellis, Ellsworth, Geary, Gove, Graham, Gray, Hamilton, Harper, Harvey, Hodgeman, Jackson, Johnson, Kingman, Kiowa, Labette, Lincoln, Linn, Lyon, McPherson, Meade, Miami, Mitchell, Montgomery, Morton, Osage, Osborne, Ottawa, Phillips, Pottawatomie, Rawlins, Reno, Republic, Rice, Riley, Rooks, Russell, Saline, Sedgwick, Seward, Shawnee, Stanton, Stevens, Sumner, Thomas, Wabaunsee, Wallace, Washington, Wichita, Wilson, and Woodson counties.

KENTUCKY: Barren, Calloway, Fayette, and Warren counties.

LOUISIANA: Jefferson Davis, Rapides, and Tangipahoa parishes.

MARYLAND: Cecil and Prince Georges counties.

MICHIGAN: Jackson, Kent, Leelanau, Van Buren, and Washtenaw counties.

MINNESOTA: Becker, Blue Earth, Brown, Chippewa, Clay, Douglas, Faribault, Fillmore, Goodhue, Houston, Kandiyohi, Lincoln, Mille Lacs, Nicollet, Olmstead, Pope, Ramsey, Scott, Stearns, Wabasha, Waseca, and Winona counties.

MISSOURI: Atchison, Audrain, Barry, Barton, Bates, Boone, Buchanan, Callaway, Cass, Cedar, Cooper, Crawford, Franklin, Greene, Henry, Hickory, Holt, Howell, Jackson, Jasper, Jefferson, Lincoln, McDonald, Nodaway, Ozark, Phelps, Pulaski, Polk, Reynolds, Ste. Genevieve, St. Louis, Shannon, Washington, Wayne, and Webster counties.

MONTANA: Yellowstone County.

NEBRASKA: Antelope, Banner, Brown, Buffalo, Cedar, Chase, Cherry, Cheyenne, Custer, Dawes, Deuel, Dodge, Franklin, Garden, Hall, Jefferson, Kearney, Lancaster, McPherson. Nuckolls, Platte, Saline, Saunders, Sheridan, Sioux, and Thomas counties.

NEW JERSEY: Passaic and Somerset counties.

NEW MEXICO: Santa Fe County.

NEW YORK: Columbia, Nassau, and Richmond counties.

NORTH CAROLINA: Durham, Orange, and Rowan counties.

NORTH DAKOTA: Benson, Burleigh, Cass, McHenry, Morton, Ransom, Richland, Sioux, and Ward counties.

OHIO: Adams, Ashtabula, Athens, Clark, Coshocton, Erie, Franklin, Guernsey, Highland, Logan, Lucas, Morgan, Noble, Ottawa, Pickaway, and Pike counties.

OKLAHOMA: Beckham, Carter, Cleveland, Comanche, Creek, Custer, Grady, Greer, Johnston, Le Flore, Logan, McClain, Murray, Oklahoma, Pawnee, Payne, Roger Mills, Rogers, Texas, and Woods counties.

PENNSYLVANIA: Bucks County.

SOUTH CAROLINA: Cherokee County.

SOUTH DAKOTA: Corson, Custer, Grant, Harding, Mellette, Pennington, Perkins, Shannon, Stanley, Todd, and Washabaugh counties.

TENNESSEE: Knox and Rutherford counties.

TEXAS: Armstrong, Bastrop, Bexar, Brewster, Calhoun, Cass, Colorado, Dallas, De Witt, Fayette, Fort Bend, Garza, Hartley, Hill, Kendall, Kerr, Potter, Randall, Tarrant, Travis, Uvalde, and Walker counties.

VIRGINIA: Arlington, Campbell, Caroline, Dinwiddie, Fairfax, Fauquier, Loudoun, Prince George, Prince William, Rockbridge, Shenandoah, and Sussex counties.

WEST VIRGINIA: Berkeley, Grant, Hampshire, Jefferson, and Morgan counties.

WISCONSIN: Columbia, Dane, Dunn, Jackson, Kenosha, Portage, Rock, Sauk, Walworth, and Wood counties.

WYOMING: Crook, Fremont, Platte, and Sheridan counties.

MEXICO: COAHUILA: Sierra de San Manuel, Monclova. NUEVO LEON: Monterrey.

Although the flowers are very uniform throughout the vast range of the species, the leaves of *A. viridiflora* are tremendously variable, as is well known. A few years ago I attempted to resolve a consistent pattern from this variability, but without success. Consequently I am not attempting to divide the species into infra-specific populations which would be arbitrary rather than natural in my opinion.

91. **ASCLEPIAS NUTTALLIANA** Torr. in Ann. Lyc. N. Y. 2:218. 1828. [T.: *James s. n.!*]

Acerates nuttalliana (Torr.) Eaton, Man. ed. 5, 90. 1829.
Polyotus lanuginosus Nutt. in Trans. Amer. Phil. Soc. n. s. 5:200. 1837, ex char. [T.: *Nuttall s. n*]
Acerates lanuginosa (Nutt.) Dcne. in DC. Prodr. 8:523. 1844.
Acerates monocephala Lapham, ex A. Gray, Man. ed. 2, Add. VI. 1857. [T.: *Lapham, s. n.*, MO!]

Low perennial herbs. Stems clustered from the rootstalk, rather slender, simple, 8–20 cm. tall, generally pilosulose. Leaves irregularly approximate, shortly petiolate to subsessile, oblong-lanceolate, apex rather abruptly obtuse or rounded, base obtuse, 4–7 cm. long, 0.7–2.2 cm. broad, firmly membranaceous, generally and rather sparsely pilosulose, particularly beneath; petioles obsolete to about 5 mm. long. Inflorescences terminal, solitary, sessile or subsessile, several- to many-flowered, pilosulose; peduncles obsolete to 3 cm. long; pedicels slender, 0.7–1.5 cm. long.

Flowers rather small; calyx lobes ovate-lanceolate, 2–3 mm. long, minutely pilosulose; corolla reflexed-rotate, pale greenish yellow sometimes slightly tinged with purple without, the lobes about 5 mm. long; gynostegium pale greenish, sessile, the hoods deeply saccate, oblongoid, about 3 mm. long, almost equalling the anther head, the anther head about 1.5 mm. long and 2 mm. broad. Follicles unknown.

Prairies, knobs, and sandhills, sometimes spreading to railways. Southern Wisconsin and northern Illinois westward to the Dakotas, Nebraska, and Kansas. Blooming from May to August.

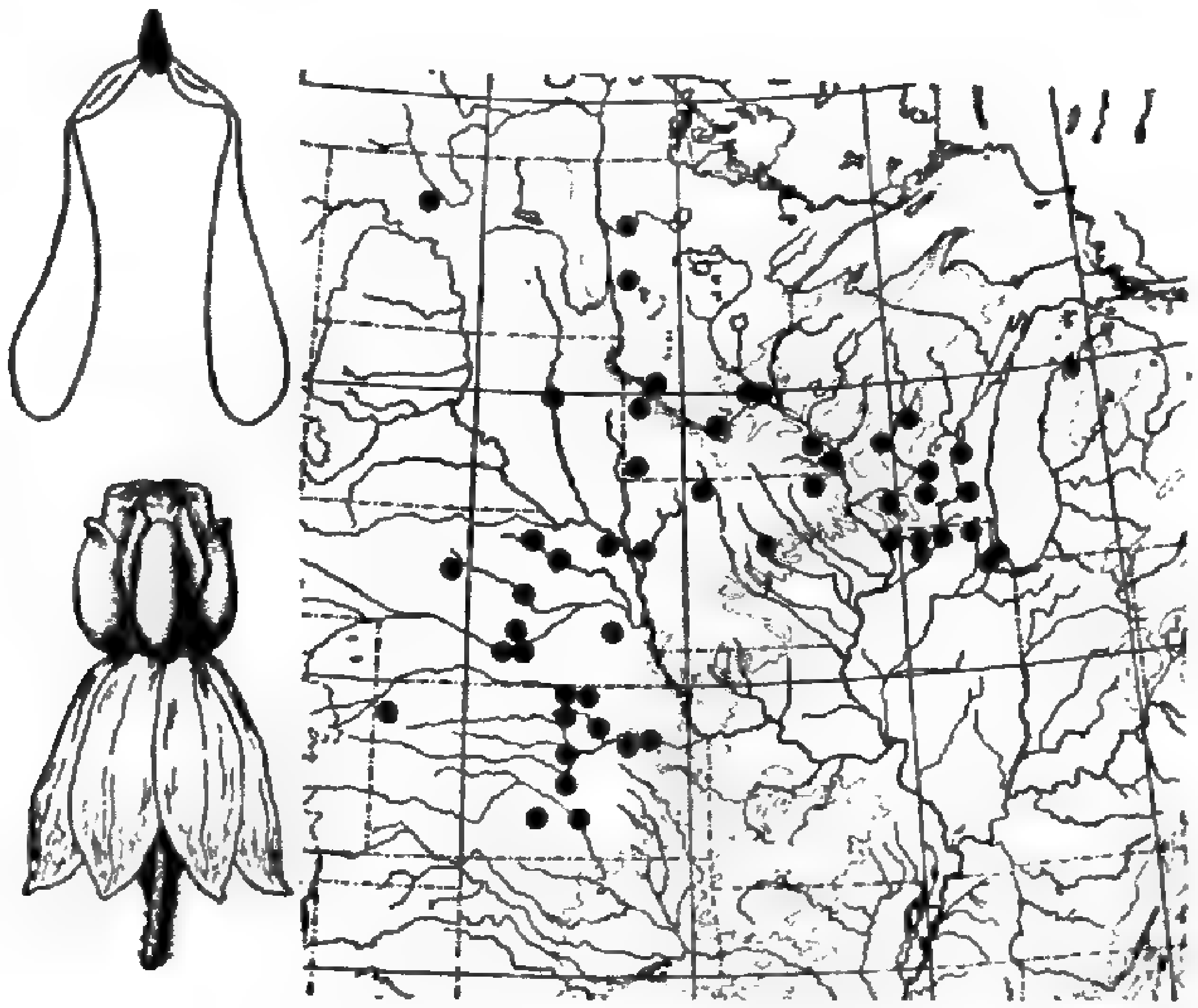

Fig. 97. *Asclepias nuttalliana* Torr.

UNITED STATES:

ILLINOIS: Boone, Cook, Du Page, Jo Daviess, McHenry, Ogle, and Winnebago counties.

IOWA: Emmet, Hardin, Winneshiek, and Woodbury counties.

KANSAS: Cloud, McPherson, Pratt, Republic, Riley, Saline, Sedgwick, Shawnee, Sherman, Wabaunsee, and Washington counties.

MINNESOTA: Chippewa, Clay, Hennepin, Houston, Nicollet, Polk, Ramsey, Rock, Winona, and Yellow Medicine counties.

NEBRASKA: Antelope, Buffalo, Dixon, Holt, Kearney, Lancaster, Phelps, Thomas, and Valley counties.

NORTH DAKOTA: Ward County.

SOUTH DAKOTA: Spink County.

WISCONSIN: Columbia, Dane, Fond du Lac, Iowa, Juneau, Portage, and Waukesha counties.

A very odd and infrequently collected species having essentially the same distribution as *A. ovalifolia* and occasionally associated with it.

SUBGENUS VI. SOLANOA (Greene) Woodson, stat. nov.

Schizonotus A. Gray, in Proc. Amer. Acad. 12:66. 1877, non Lindl. [T.: *S. purpurascens* A. Gray]

Solanoa Greene, Pittonia 2:67. 1890. [Based on *Schizonotus* A. Gray]
Solanoana O. Ktze. Rev. Gen. 2:421. 1891. [Based on *Solanoa* Greene]

KEY TO THE SPECIES

a. Flowers relatively large, the corolla lobes about 1.0–1.5 cm. long; anther wings salient at the base.
  b. Plants very densely arachnoid-tomentose, relatively stout, 2–9 dm. tall; hoods not wholly adnate to the column, broadly rounded at the tip, lower than the anther head. Central and southern California ....92. *A. californica*
  bb. Plants essentially glabrous, relatively slender, about 1–3 dm. tall; hoods wholly adnate to the column, abruptly 2-apiculate, as tall as the anther head or somewhat taller. Western Wyoming and Colorado to eastern Oregon and California................93. *A. cryptoceras*
aa. Flowers relatively small, the corolla lobes about 5 mm. long; anther wings salient somewhat above the middle; hoods almost wholly adnate to the column, broadly rounded, much lower than the anther head; plants relatively slender, densely puberulent, about 1–3 dm. tall. Northern California ....94. *A. solanoana*

92. ASCLEPIAS CALIFORNICA Greene, in Erythea 1:92. 1893. [Based on *Acerates tomentosa* Torr.]

Acerates tomentosa Torr. Bot. Mex. Bound. Surv. 160. 1859, non *Asclepias tomentosa* Ell. [T.: *Parry s. n.*, MO!]
Gomphocarpus tomentosus (Torr.) A. Gray, Bot. Calif. 1:477. 1876, non Burch.
Gomphocarpus torreyi Macbr. in Contr. Gray Herb. no. 65:42. 1922. [Based on *Acerates tomentosa* Torr.]

Herbaceous perennials very conspicuously white arachnoid-tomentose throughout. Stems erect, ascending, or somewhat decumbent, rather stout, simple or branching from the caudex, 2–9 dm. tall. Leaves opposite, subsessile or shortly petiolate, broadly ovate or oval to elliptic-lanceolate, apex acute to obtuse, base usually broadly cordate, 4–16 cm. long, 2.5–7.0 cm. broad, firmly membranaceous,

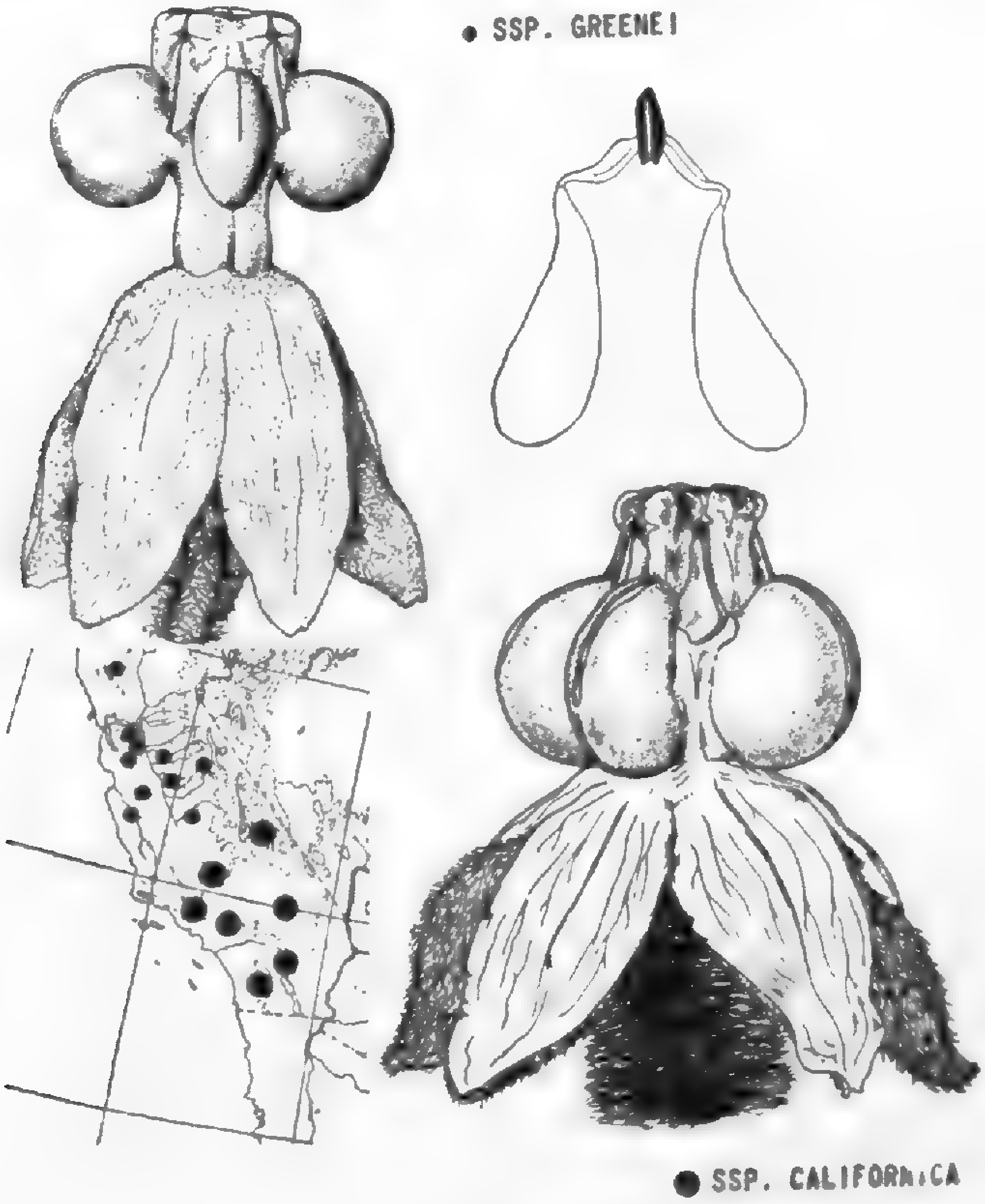

Fig. 98. *Asclepias californica* Greene

more or less glabrate in age; petioles obsolete to 2 cm. long. Inflorescences terminal or subterminal and lateral at rather few of the uppermost nodes, subsessile to definitely pedunculate, several-flowered; peduncles obsolete to 3 cm. long, relatively stout; pedicels more slender, 2–4 cm. long. Flowers rather large; calyx lobes ovate to lanceolate, about 4 mm. long, densely white-tomentulose without; corolla reflexed-rotate, purple, densely tomentulose without, the lobes 1.0–1.2 cm. long; gynostegium subsessile to definitely stipitate, purplish rose, the hoods deeply saccate, calceolate, ovoid, 4–5 mm. long, the horn very minute or absent, the anther head about 3 mm. long and 5 mm. broad. Follicles erect on deflexed pedicels, rather broadly fusiform, rather gradually apiculate, 8–10 cm. long, 2.0–2.5 cm. thick, densely white-tomentose; seeds broadly oval, about 1 cm. long, the white coma about 2 cm. long.

KEY TO THE SUBSPECIES

Gynostegium appearing subsessile, the hoods strongly pendulous at the base. Southern California ....92a. *A. californica californica*

Gynostegium obviously stipitate, the hoods scarcely pendulous at the base. Northern California ....92b. *A. californica greenei*

92a. ASCLEPIAS CALIFORNICA ssp. CALIFORNICA.

Gomphocarpus tomentosus var. *xanti* A. Gray, Bot. Calif. 1:477. 1876, ex char. [T.: *Xantus s. n.*]

Gomphocarpus torreyi var. *xanti* (A. Gray) Macbr. in Contr. Gray Herb. no. 65:42. 1922.

Dry clearing, brushy hillsides, Mohave Desert. Southern California; Baja California. Blooming from April to July.

UNITED STATES:

CALIFORNIA: Inyo, Kern, Los Angeles, Riverside, San Bernardino, San Diego, and Ventura counties.

92b. ASCLEPIAS CALIFORNICA ssp. **greenei** Woodson, subspec. nov.

A subspecie typica columna gynostegii aperta cylindrica cucullis minus saccatis differt.—Typus: *A. A. Heller 8596* in Herb. Missouri Bot. Gard. ("Hall's Valley, on the Mt. Hamilton road, Santa Clara County, California, May 30, 1907").

Flats, grassy hillsides, brushy slopes, Upper Sonoran. Northern California. Blooming from April to June.

UNITED STATES:

CALIFORNIA: Alameda, Contra Costa, Fresno, Lake, Mariposa, Merced, Monterey, San Benito, Santa Clara, and Stanislaus counties.

These subspecies intergrade to some extent, and the differences which separate them are rather technical. However, they certainly are of importance phylogenetically and should be named as populations.

93. ASCLEPIAS CRYPTOCERAS S. Wats. Bot. King's Exped. 283, *t. 28.* 1871. [T.: *Nuttall s. n.*, NY!]

Decumbent herbaceous perennials. Stems clustered from the base, somewhat stout, more or less ancipitous or flattened, simple or branching from the very base, 1–3 dm. long, glabrous or essentially so. Leaves opposite, shortly petiolate, very

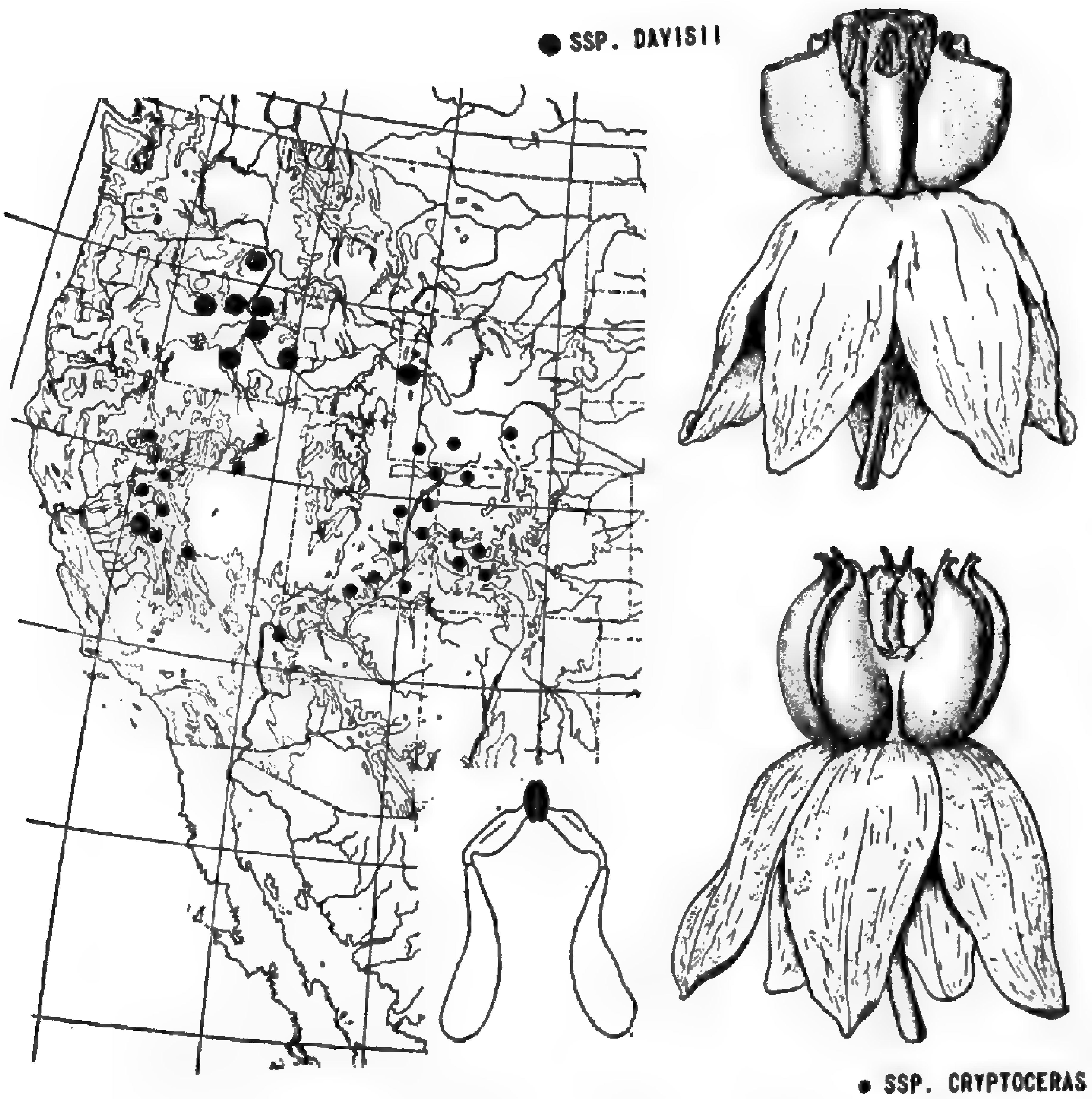

Fig. 99. *Asclepias cryptoceras* S. Wats.

broadly oval or ovate, suborbicular, apex broadly rounded to very broadly obtuse, base broadly rounded to very slightly cordate, 4–9 cm. long, 4–8 cm. broad, glaucous, glabrous; petioles nearly obsolete to 5 mm. long. Inflorescences terminal and frequently lateral at the uppermost nodes, the lateral sessile, rather few- to several-flowered; peduncles obsolete to 7 cm. long when terminal; pedicels slender, 2–4 cm. long, glabrous. Flowers large; calyx lobes narrowly lanceolate, 6–7 mm. long, glabrous; corolla reflexed-rotate, greenish yellow, the lobes 1.0–1.5 cm. long; gynostegium sessile, pale rose, the hoods deeply saccate and decurrent upon the column, conspicuously 2-apiculate, 6–9 mm. long, equalling the anther head or somewhat longer, the horn very inconspicuous and incurved or absent, the anther head 3.0–3.5 mm. long and 4–5 mm. broad. Follicles erect on erect pedicels, broadly fusiform, rather shortly apiculate, 4–7 cm. long, 1.5–2.5 cm. broad, smooth, glabrous; seeds broadly oval, about 1 cm. long, the pale tawny coma 1.5–2.5 cm. long.

KEY TO THE SUBSPECIES

Hoods oblong-ovoid, gradually rounded to the tips, usually somewhat surpassing the anther head. Western Colorado, Utah, and adjacent Wyoming, Arizona, and eastern California ....93a. *A. cryptoceras cryptoceras*

Hoods subrhombic, truncate to the tips, usually somewhat shorter than the anther head. Southern Idaho and adjacent Wyoming, Oregon, and California............93b. *A. cryptoceras davisii*

The differences between these two subspecies are similar to those of *A. vestita* and *A. californica:* the extremes so distinct in floral structures as to be interpreted as species, but with geographical intergradation.

Watson's original sheet of *A. cryptoceras* bears four different collections: one collected by Watson from the "W. Humboldt Mtns., Nev." and one from "Idaho, Rev. R. D. Nevins, 1876", both of which are ssp. *davisii;* one from Glenwood, Utah, collected in May, 1875 by L. F. Ward in fruit, and one collected by Nuttall on "Ham's Fork of the . . . . [Green River, Utah]" are ssp. *cryptoceras.* In proposing *A. cryptoceras* Watson cites the Nuttall specimen first, secondly a specimen collected by Fremont *(584)* in southeastern Idaho (which is not represented), and thirdly the Watson specimen. I am choosing the Nuttall specimen as the lectotype. The highly formalized drawing is rather a composite of both subspecies.

93a. ASCLEPIAS CRYPTOCERAS ssp. CRYPTOCERAS.

Acerates latifolia Torr. & Frem. in Rept. Frem. Exped. 317. 1845, non *Asclepias latifolia* Raf. [T.: *Fremont s. n.*, NY!]

Loose shaly, sandy, and clay hillsides, bottoms of washes and canyons, arid plains. Western Colorado, Utah, and adjacent Wyoming, Arizona, and California. Blooming from April to June.

UNITED STATES:
ARIZONA: Mohave County.
CALIFORNIA: Mono County.
COLORADO: Delta, Mesa, Moffat, Montrose, and Ouray counties.
NEVADA: Churchill, Douglas, Elko, Esmeralda, Eureka, Humboldt, Lyon, Mineral, and Washoe counties.
UTAH: Carbon, Daggett, Emery, Garfield, Grand, Kane, San Juan, and Uintah counties.
WYOMING: Carbon, Sweetwater, and Uinta counties.

93b. ASCLEPIAS CRYPTOCERAS ssp. davisii (Woodson) Woodson, stat. nov.

Asclepias davisii Woodson, in Ann. Missouri Bot. Gard. 26:261, *fig. 1.* 1939. [T.: *Davis 85*, MO!]

Barren clay knolls, loose shale and lava hillsides. Southern Idaho and adjacent Wyoming, Oregon, and California.

UNITED STATES:
CALIFORNIA: Mono County.
IDAHO: Canyon, Elmore, and Washington counties.
OREGON: Baker, Grant, Malheur, and Wallowa counties.
WYOMING: Lincoln County.

94. ASCLEPIAS SOLANOANA Woodson, in Ann. Missouri Bot. Gard. 28:207. 1941. [Based on *Gomphocarpus purpurascens* A. Gray, non Rich.]

Gomphocarpus purpurascens A. Gray, in Proc. Amer. Acad. 10:76. 1874, non A. Rich. [T.: *Towle s. n.*, GH!]
Schizonotus purpurascens (A. Gray) A. Gray, loc. cit. 12:66. 1877.
Solanoa purpurascens (A. Gray) Greene, Pittonia 2:67. 1890.
Solanoana purpurascens (A. Gray) O. Ktze. Rev. Gen. 2:421. 1891.

Prostrate herbaceous perennials. Stems relatively slender, simple, 1.0–2.5 dm. long, densely and minutely puberulent. Leaves opposite, petiolate, broadly ovate or oval, apex broadly obtuse or rounded, base truncate to broadly cordate, 3–4 cm. long, 2.5–3.0 cm. broad, firmly membranaceous or somewhat subsucculent, densely and minutely puberulent particularly below; petioles 0.5–2.0 cm. long. Inflorescences terminal or subterminal, solitary or lateral also at the uppermost nodes, many-flowered, pedunculate, densely and minutely puberulent; peduncles 1.5–4.5 cm. long; pedicels 1.0–1.5 cm. long. Flowers small; calyx lobes narrowly lanceolate, about 3 mm. long, very minutely puberulent; corolla reflexed-rotate, purple, the lobes about 6 mm. long; gynostegium sessile, cream, the hoods almost wholly adnate to the column, completely bifid dorsally, rhombic-ovoid, about 2–3 mm. long, inserted below the anther head, the horn absent, the anther head about 1.5 mm. long and broad. Follicles erect on deflexed pedicels, rather narrowly fusiform, gradually apiculate, about 10 cm. long and 0.5 cm. thick; seeds unknown.

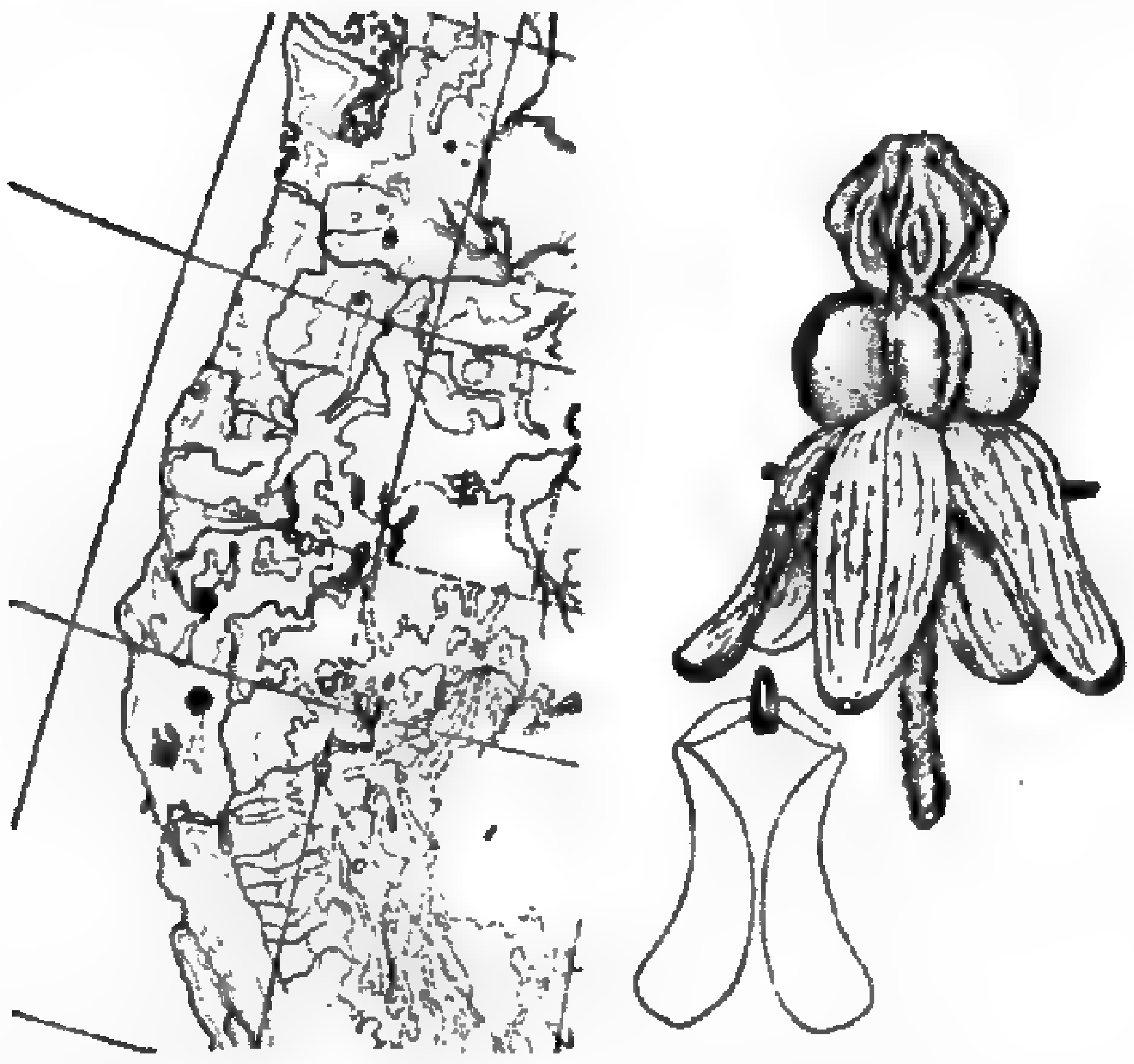
Fig. 100. *Asclepias solanoana* Woods.

Open woods, rocky slopes on serpentine. Northern California. Blooming in June.

United States:

california: Colusa, Sonoma, and Trinity counties.

subgenus VII. Polyotus (Nutt.) Woodson, stat. nov.

Polyotus Nutt. in Trans. Amer. Phil. Soc. n. s. 5:199. 1837. [T.: *P. angustifolius* Nutt.]

KEY TO THE SPECIES

a. Leaves rather strictly ascending; hoods about as long as the anther head, deeply 2-lobed, the wholly adnate crest forming a third, median lobe; anther wings very prominently spurred toward the base; follicles erect on erect pedicels. Southwestern Missouri westward to South Dakota, eastern Colorado, and northern Texas............................95. *A. stenophylla*

aa. Leaves widely spreading to somewhat reflexed; hoods shorter than the anther head, broadly emarginate to essentially entire.

  b. Anther head truncate-conic, the wings definitely salient and conspicuously spurred at the base; hoods with a minute horn or crest toward the base. Arizona and adjacent Utah ....96. *A. rusbyi*

  bb. Anther head depressed-spheric, the wings rather symmetrically arcuate and not spurred at the base; hoods without a horn or crest; follicles erect on deflexed pedicels. Nebraska to Texas and westward to southern Arizona; northern Coahuila..............97. *A. engelmanniana*

95. Asclepias stenophylla A. Gray, in Proc. Amer. Acad. 12:72. 1877. [Based on *Polyotus angustifolius* Nutt.]

Polyotus angustifolius Nutt. in Trans. Amer. Phil. Soc. n. s. 5:201. 1837, nec *Asclepias angustifolia* Schweig. nec alior. [T.: *Nuttall s. n.*, MO photo!]

Acerates angustifolia (Nutt.) Dcne. in DC. Prodr. 8:522. 1844.

Herbaceous perennials from subnapiform tuberous rootstalks. Stems rather slender, simple, 2–8 dm. tall, very minutely puberulent to glabrate. Leaves irregularly approximate, sessile, linear, 6–14 cm. long, 2–4 mm. broad, rather strictly ascending, firmly membranaceous, very minutely and scatteringly puberulent to glabrate. Inflorescences lateral at few to several of the uppermost nodes, several-flowered, subsessile to very shortly pedunculate; peduncles obsolete to 1 cm. long, minutely puberulent; pedicels very slender, 5–8 mm. long, minutely puberulent. Flowers rather small; calyx lobes lanceolate, about 2–3 mm. long, minutely puberulent; corolla rotate, pale greenish white or yellow, the lobes about 6 mm. long; gynostegium sessile, pale greenish cream or white, the hoods saccate and strongly adnate to the column, conspicuously excurrent-auriculate at the base, oblong-elliptic, 3–4 mm. long, the tip deeply 2-lobed, the wholly adnate horn or crest forming a third, lower, median lobe, the anther head broadly truncate-conic, about 2 mm. long and broad. Follicles erect on erect pedicels, very narrowly fusiform and gradually attenuate, 9–12 cm. long, about 7–8 mm. thick, minutely pilosulose to glabrate; seeds oval, 5–6 mm. long, the pale tawny coma 3.0–3.5 cm. long.

Prairies and limestone glades. Southwestern Missouri westward to South Dakota, eastern Colorado, and northern Texas. Blooming from June to August.

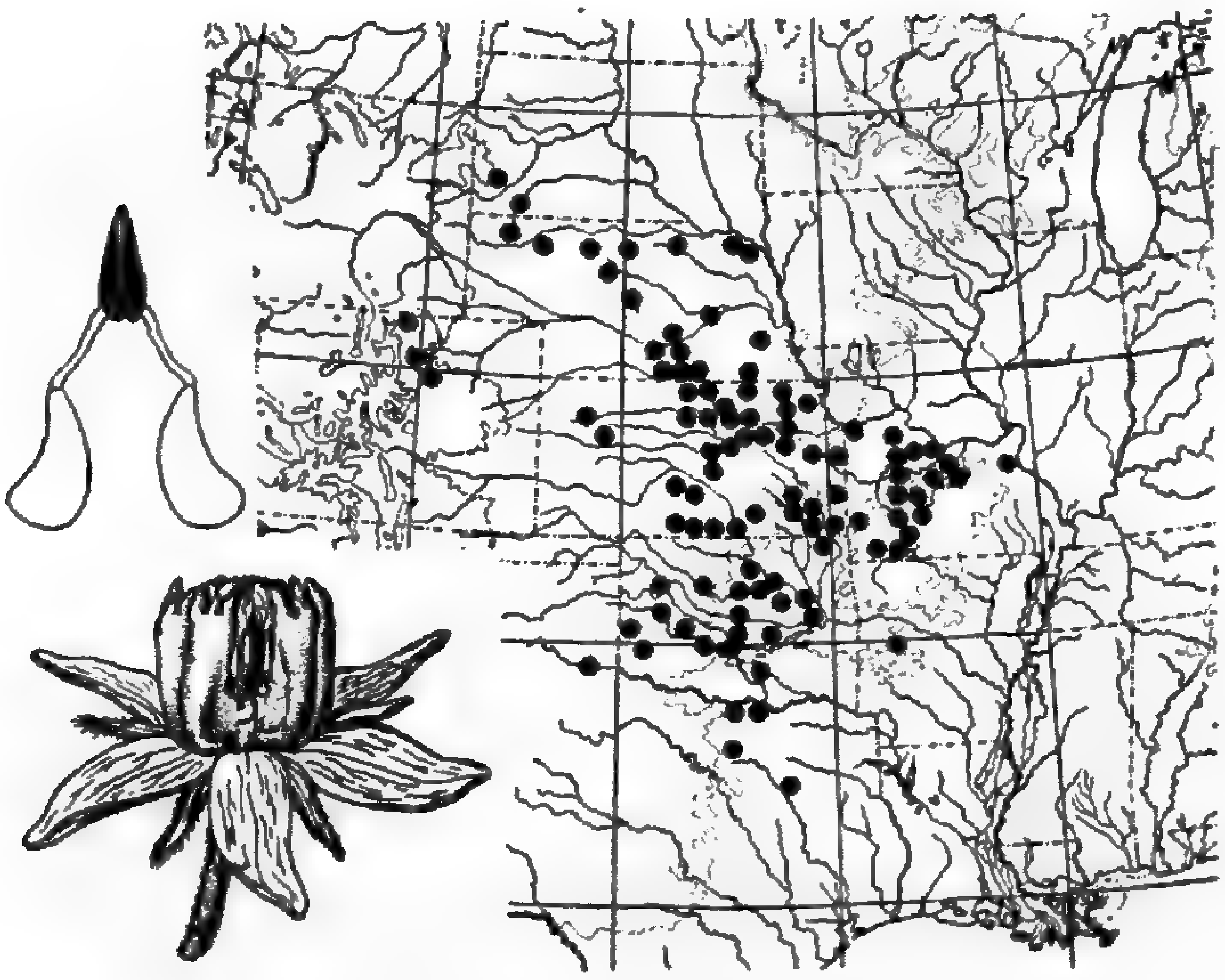

Fig. 101. *Asclepias stenophylla* A. Gray

United States:

ARKANSAS: Yell County.

COLORADO: Boulder, Denver, and Larimer counties.

KANSAS: Atchison, Barber, Bourbon, Cherokee, Clay, Cowley, Dickinson, Elk, Ellsworth, Franklin, Geary, Gove, Harper, Jackson, Jewell, Labette, Lincoln, McPherson, Miami, Mitchell, Morris, Nemaha, Neosho, Osage, Osborne, Reno, Republic, Rice, Riley, Rooks, Russell, Saline, Shawnee, Smith, Stafford, Sumner, Thomas, Wabaunsee, Washington, Wilson, and Woodson counties.

MISSOURI: Barry, Benton, Christian, Cole, Dallas, Greene, Hickory, Jackson, Jasper, Jefferson, Maries, Morgan, Pettis, Phelps, Polk, Pulaski, Stone, and Webster counties.

NEBRASKA: Brown, Buffalo, Cedar, Cherry, Custer, Dawes, Dixon, Franklin, Holt, Jefferson, Kearney, Lancaster, Merrick, Nuckolls, Phelps, Sheridan, Thomas, and Webster counties.

OKLAHOMA: Beckham, Caddo, Cleveland, Comanche, Craig, Creek, Custer, Dewey, Grady, Greer, Johnston, Kingfisher, Logan, McClain, Muskogee, Noble, Oklahoma, Pawnee, Payne, Seminole, and Wagoner counties.

SOUTH DAKOTA: Custer and Shannon counties.

TEXAS: Cooke, Grayson, Hall, Henderson, and Tarrant counties.

Asclepias stenophylla long has been prominent as a "link" between the genera *Asclepias (sensu stricto)* and *Acerates (sensu lato)*, because of its saccate hoods with their obvious crests or horns. The combination of these characters is repeated periodically throughout the inclusive genus *Asclepias* and renders them particularly useless in the segregation of natural genera.

96. ASCLEPIAS **rusbyi** (Vail) Woodson, comb. nov.

Acerates rusbyi Vail, in Bull. Torrey Bot. Club 25:37. 1898. [T.: *Rusby s. n.*, NY!]
Asclepias engelmanniana var. *rusbyi* (Vail) Kearney, in Leafl. West. Bot. 5:197. 1949.

Herbaceous perennials. Stems rather slender, simple, glaucous, glabrous. Leaves irregularly approximate, sessile, linear, 9–15 cm. long, 3–7 mm. broad, somewhat subsucculent, glaucous, glabrous, laxly spreading to reflexed, more or less conduplicate. Inflorescences lateral from few to several of the upper nodes, several- to rather many-flowered, subsessile to shortly pedunculate; peduncles obsolete to 1.5 cm. long, glabrous or essentially so; pedicels slender, about 1 cm. long, inconspicuously pilosulose. Flowers rather small; calyx lobes ovate-lanceolate, about 3–4 mm. long, minutely and rather irregularly pilosulose; corolla rotate, pale green usually somewhat tinted with purple without, the lobes 5–6 mm. long; gynostegium sessile or subsessile, pale green somewhat tinted with purple, the hoods deeply saccate and excurrently auriculate at the base, 2.0–2.5 mm. long, truncate, with an inconspicuous adnate crest of about equal length, the anther head truncately conic, about 3 mm. long and broad. Follicles unknown.

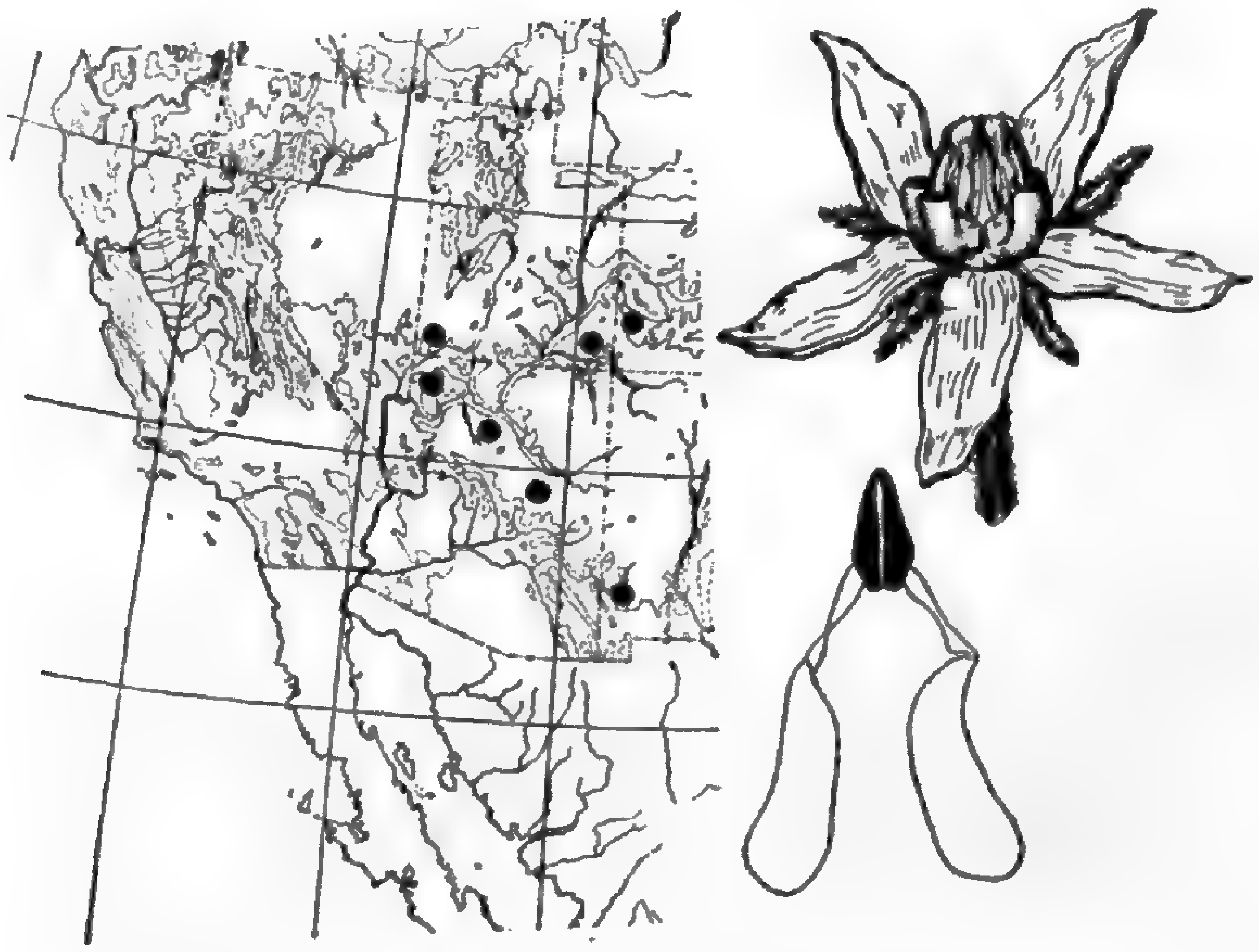

Fig. 102. *Asclepias rusbyi* (Vail) Woods.

Rocky slopes in open oak forest. Northern Arizona and adjacent Utah. Blooming in June and July.

United States:
arizona: Coconino, Gila, and Mohave counties.
utah: San Juan and Washington counties.

When I first examined the type specimen of *A. rusbyi,* I fancied that it might represent a hybrid between *A. engelmanniana* and *A. stenophylla,* because of a combination of resemblances to those species. This can scarcely be the case, however, since it is far outside the present range of *A. stenophylla.* Another possible interpretation is that it is a subspecies of *A. engelmanniana,* which is essentially Kearney's position. I am rather reluctantly assigning it to full status as a species because there are several, not merely one or at best a few, structural differences of the flowers, and because the population occurs well within the range of *A. engelmanniana.*

97. **Asclepias engelmanniana** Woodson, in Ann. Missouri Bot. Gard. 28:207. 1941. [Based on *Acerates auriculata* Engelm.]

Acerates auriculata Engelm. in Torr. Rept. Bot. Mex. Bound. Surv. 160. 1859. [T.: *Bigelow s. n.,* US!]
Asclepias auriculata (Engelm.) Holzinger, in Bot. Gaz. 17:125, 160. 1892, non HBK.
Gomphocarpus auriculatus (Engelm.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4^2:236. 1895.

Herbaceous perennials. Stems rather stout, simple or branching infrequently from the caudex, 6–12 dm. tall, glabrous or essentially so. Leaves irregularly approximate, sessile, linear, 12–18 cm. long, 1.5–3.0 mm. broad, rather laxly spreading or reflexed, more or less canaliculate, firmly membranaceous or somewhat subsucculent, glabrous. Inflorescences lateral from several to many of the upper nodes, many-flowered and very crowded, subsessile to shortly pedunculate; peduncles

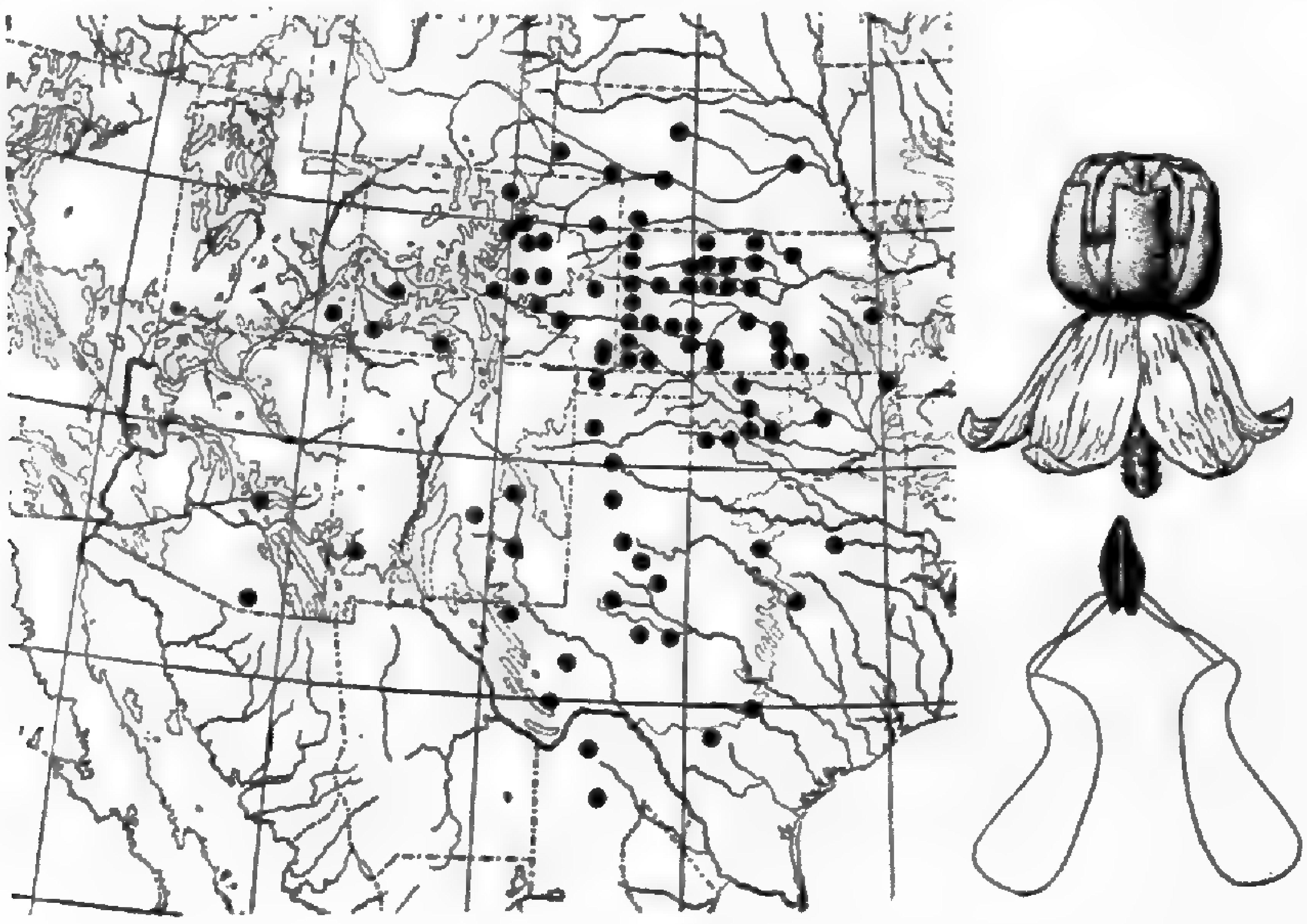

Fig. 103. *Asclepias engelmanniana* Woods.

obsolete to about 2 cm. long, relatively stout, very inconspicuously appressed-puberulent; pedicels rather slender, about 1 cm. long, inconspicuously appressed-puberulent. Flowers rather small; calyx lobes ovate-lanceolate, about 3 mm. long, essentially glabrous; corolla reflexed-rotate, pale green more or less flushed with purple without, the lobes about 5 mm. long; gynostegium sessile, the hoods deeply saccate and excurrently auriculate at the base, broadly truncate or broadly retuse at the tip, about 3 mm. long, without a horn, the anther head depressed-spheric, about 2.5 mm. long and 3 mm. broad. Follicles erect on deflexed pedicels, narrowly fusiform, gradually attenuate, 8–12 cm. long, about 1.5 cm. thick; seeds oval, about 7 mm. long, the pale tawny coma about 3 cm. long.

Prairies and swales, open sandy hillsides, draws, washes, and bottoms. Nebraska to Texas and westward to Arizona; Coahuila. Blooming from July to September.

UNITED STATES:

ARIZONA: Gila and Santa Cruz counties.

COLORADO: Arapahoe, Archuleta, Baca, Boulder, Cheyenne, Denver, El Paso, Fremont, Jefferson, Larimer, Montezuma, Montrose, Otero, Prowers, Pueblo, Teller, and Yuma counties.

KANSAS: Anderson, Cheyenne, Cloud, Comanche, Cowley, Ellis, Finney, Ford, Gove, Graham, Greeley, Hamilton, Harvey, Hodgeman, Kearney, Kiowa, Logan, Morton, Norton, Osborne, Rooks, Russell, Sedgwick, Sheridan, Sherman, Smith, Stafford, Stanton, Stevens, Sumner, Trego, and Wallace counties.

NEBRASKA: Banner, Deuel, Dundy, Lincoln, Platte, and Thomas counties.

NEW MEXICO: Chaves, De Baca, Grant, and Lincoln counties.

OKLAHOMA: Blaine, Custer, Cimarron, Kingfisher, Major, Ottawa, Payne, Roger Mills, and Woods counties.

TEXAS: Brewster, Collin, Comal, Culberson, Garza, Hartley, Irion, Lubbock, Martin, Oldham, Palo Pinto, Pecos, Randall, Somervell, Scurry, Tom Green, and Uvalde counties.

MEXICO: COAHUILA: Múzquiz, Santa Rosa Mtns.

The anther head of *A. engelmanniana* is most unique: depressed-spheric with the broadly lunate anther wings nearly describing its circumference and the large glands of the translators virtually meeting at the summit.

SUBGENUS VIII. ASCLEPIODORA (A. Gray) Woodson, stat. nov.

Asclepiodora A. Gray, in Proc. Amer. Acad. 12:66. 1877. [T.: *A. viridis* (Walt.) A. Gray]

KEY TO THE SPECIES

a. Corolla lobes at length reflexed; hoods only slightly deflexed from the anther head; leaves opposite, deeply cordate, sessile and amplexicaul. Southwestern Texas and southern New Mexico and Arizona; Nuevo Leon to Sonora and southward to Chiapas; Guatemala .... 98. *A. elata*

aa. Corolla lobes spreading or somewhat ascending at the tips; hoods sharply deflexed from the anther head.

  b. Leaves opposite; inflorescences lateral to subterminal.

    c. Leaves broadly ovate-elliptic, deeply cordate and amplexicaul; corolla greenish white or yellow. Chihuahua .... 99. *A. mirifica*

    cc. Leaves linear-lanceolate to filiform, attenuate at the base; corolla usually strongly suffused with reddish purple.

      d. Plants herbaceous, branching infrequently; leaves rather long, linear to linear-lanceolate; inflorescences several-flowered; obviously pedunculate.

e. Hoods with conspicuous sharply ascending tips about as long as the anther head. Hidalgo and Mexico westward to Jalisco ....100. *A. fournieri*

ee. Hoods reduced to the deflexed base, without conspicuous ascending tips. Nuevo Leon and Coahuila ....101. *A. zanthodacryon*

dd. Plants suffruticose, branching repeatedly and rather fastigiately; leaves rather short, filiform; inflorescences 1-flowered, without a peduncle. Southwestern Texas ....102. *A. sperryi*

bb. Leaves irregularly approximate; inflorescences terminal.

c. Hoods less than half as long as the corolla lobes; anther head about as long as broad, the wings very narrow and inconspicuous. Tennessee to Florida and westward to Nebraska and eastern Texas ....103. *A. viridis*

cc. Hoods almost as long as the corolla lobes; anther head much broader than long, the wings very broad and conspicuous. Southern Kansas to Texas and westward to Arizona and adjacent Nevada and California; Tamaulipas to Chihuahua and southward to Hidalgo ....104. *A. asperula*

98. Asclepias elata Benth. Pl. Hartw. 290. 1848. [T.: *Hartweg s. n.*, K!]

Asclepias glaucescens var. *elata* (Benth.) Fourn. in Ann. Sci. Nat. Bot. Ser. VI, 14:382. 1882.

Asclepias macroura A. Gray, in Proc. Amer. Acad. 22:436. 1887. [T.: *E. Palmer 344*, GH!]

Herbaceous perennials. Stems rather stout, simple, 3–7 dm. tall, glabrous, glaucous. Leaves opposite, sessile, very broadly oval to oblong, apex very broadly obtuse to rounded, base broadly cordate, 7–14 cm. long, 2.5–7.0 cm. broad, glabrous, very glaucous. Inflorescences terminal or subterminal and usually lateral from few of the uppermost nodes, several- to rather many-flowered, rather long-pedunculate; peduncles relatively stout, glabrous or very inconspicuously pilosulose in opposed lines; pedicels more slender, 1.5–3.0 cm. long, densely white-tomentu-

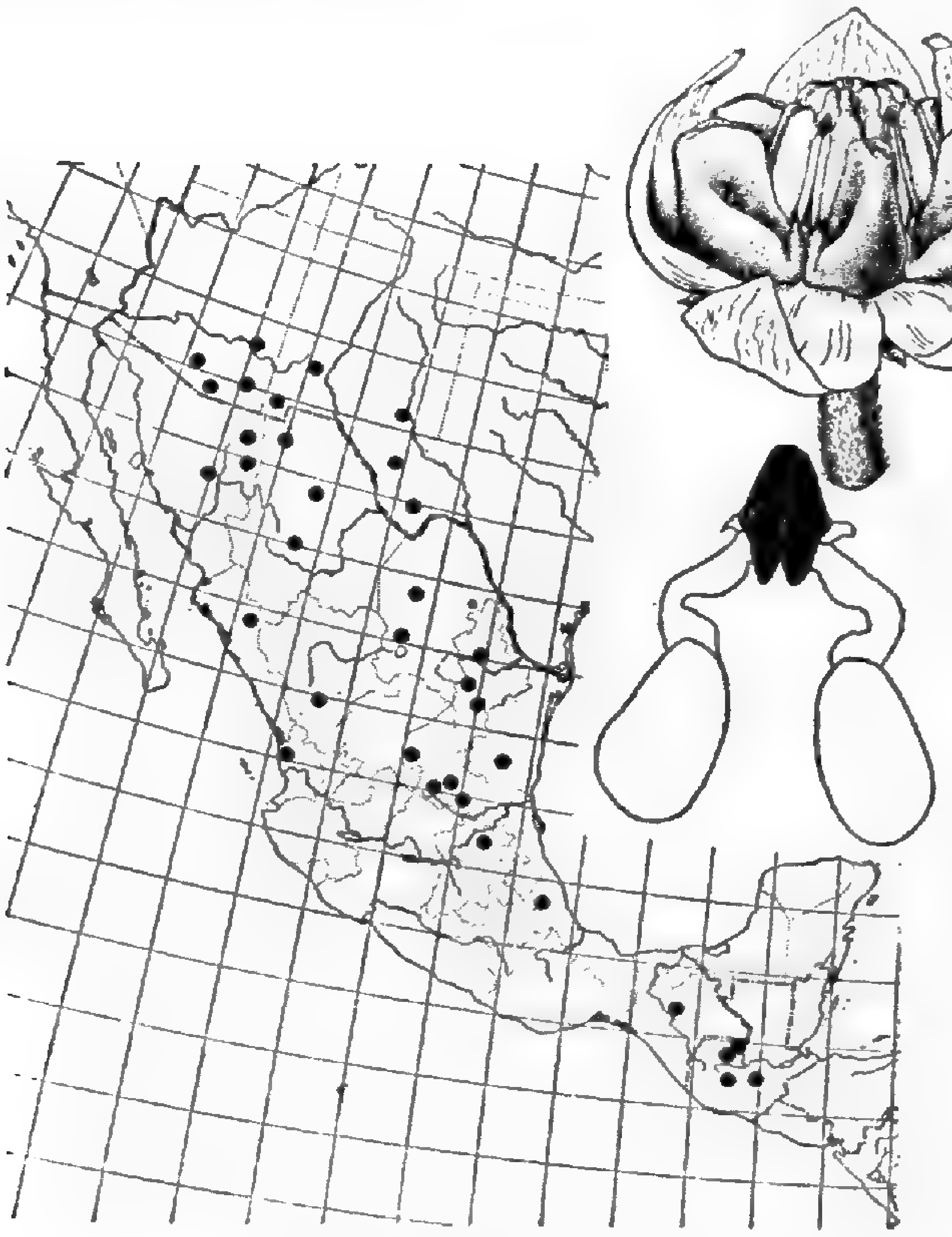

Fig. 104. *Asclepias elata* Benth.

lose. Flowers rather large; calyx lobes ovate, 3–4 mm. long; corolla pale green or greenish white, the lobes 8–12 mm. long; gynostegium sessile, greenish white to cream, the hoods saccate at the base, compressed-rhomboid, 4–6 mm. long, truncate, somewhat deflexed from the anther head, the crest wholly adnate and about as long as the hood, the anther head broadly truncate-conic, about 3 mm. long and 4 mm. broad. Follicles erect on deflexed pedicels, fusiform, rather narrowly apiculate, 8–12 cm. long, 1.0–2.5 cm. thick, smooth, very inconspicuously pilosulose to glabrate; seeds oval, about 7 mm. long, the pale tawny coma 2.5–4.5 cm. long.

Dry rocky slopes in open pine, juniper, or oak woods, spreading to pastures, cultivated fields, and along railways. Southwestern Texas and southern New Mexico and Arizona; Nuevo Leon to Sonora and southward to Chiapas; Guatemala. Blooming from June to September.

UNITED STATES:
ARIZONA: Cochise, Graham, Pima, and Santa Cruz counties.
NEW MEXICO: Eddy, Hidalgo, and Sierra counties.
TEXAS: Brewster and Jeff Davis counties.

MEXICO: CHIAPAS: locality unknown. CHIHUAHUA: Janos, Carretas, Cusi, Chihuahua. COAHUILA: Santa Rosa Mtns., Parras. DURANGO: Otinapa. HIDALGO: Jacala. NAYARIT: Tepic. NUEVO LEÓN: Galeana, Saltillo, Dulces Nombres. SONORA: Bavispe, Las Cuevas, Aribabi. SINALOA: Sierra Surotato. TAMAULIPAS: Jaumave. SAN LUIS POTOSÍ: Morales, San Luis Potosí, Minas de San Rafael, Bagre. VERACRUZ: Orizaba.

GUATEMALA: HUEHUETENAGO: Huehuetenango, San Sebastián H. JALAPA: Fiscal. SOLOLA: San Pedro.

The distinction between *A. glaucescens* and *A. elata* long has been very obscure, and some authors have considered them as a single species. I have come to the conclusion that they are quite distinct, although capable of hybridization. When not in flower, the two are virtually indistinguishable, and under such conditions, in fact, the two might also be indistinguishable from other species such as *A. mirifica* or even *A. grandiflora*.

In flower, however, many differences are observable, such as the apparent column and the conspicuously exserted corona horns of *A. glaucescens*, and the sessile gynostegium and poorly developed horns of *A. elata*. According to my observations, the two species are not referable even to the same subgenera: *glaucescens* to subgen. ASCLEPIAS series GRANDIFLORAE because of the substipitate hoods and relatively narrow anther head, and *elata* to subgen. ASCLEPIODORA because the hoods are quite sessile and saccate at the base. An additional differentium is found in the translators of the two species: those of *elata* bearing two hyaline appendages from the gland just above the attachment of the translator arms, whilst such appendages are lacking in *A. glaucescens*.

As happens with embarrassing frequency in my system of *Asclepias*, however, *A. glaucescens* and *A. elata* appear to hybridize occasionally none the less, and such individuals are represented in my opinion by Gray's *A. macroura*. In interpreting such putative hybrids, one is grateful for the hyaline translator appendages of *A. elata!* Perhaps it would be better to abandon the rather fine structural distinctions which I have tried to draw between my subgenera and series, and to classify both *A. glaucescens* and *A. elata* with the species of series ROSEAE of subgenus ASCLEPIAS. Such a course, however, would immediately submerge the distinction of *Asclepiodora* even as a subgenus, and concomitant erosion of the other subgenera and series would reduce the whole to the rather amorphous genetic reticulum, which apparently it is in fact.

99. ASCLEPIAS **mirifica** Woodson, spec. nov.

Herbae perennes ca. 1 m. altae omnino glaucescentes pedicellis exceptis glabrae. Caules validi simplices. Folia opposita sessilia ovata vel ovato-elliptica apice obtusa vel late acuta basi late cordata ibique valde amplexicaulia 7–10 cm. longa 4–5 cm. lata. Inflorescentiae e nodis pluribus laterales pluriflorae longe pedunculatae; pedunculis validiusculis, 9–10 cm. longis; pedicellis graciliusculis 2–3 cm. longis sparse pilosulis. Flores magni; calycis laciniis ovatis ca. 9 mm. longis glabris purpureis; corolla rotata pallide gilva, lobis ca. 1.5 cm. longis patulis; gynostegio sessile lacteo, cucullis a gynostegio valde deflexis late subfalcatis basi saccatis ca. 6 mm. longis, crista humili vix aperta, androecio late subcylindrico ca. 4.5 mm. longo 6 mm. lato. Folliculi mihi ignoti.—Holotypus: *H. S. Gentry 2352* in Herb. Chicago Nat. Hist. Mus. ("Guasaremos, Río Mayo, Chihuahua, Mexico, infrequent herb of the cool mountain slopes, about a meter high; Upper Sonoran; oak slope; July 30, 1936.").

I could choose an even more dramatic epithet to describe my horror when the nature of this strange plant finally dawned upon me, for I had at first assigned it to *A. elata,* as the general appearance would suggest. The flowers are totally different, as the key and description convey; close relationship to *elata* is implied by

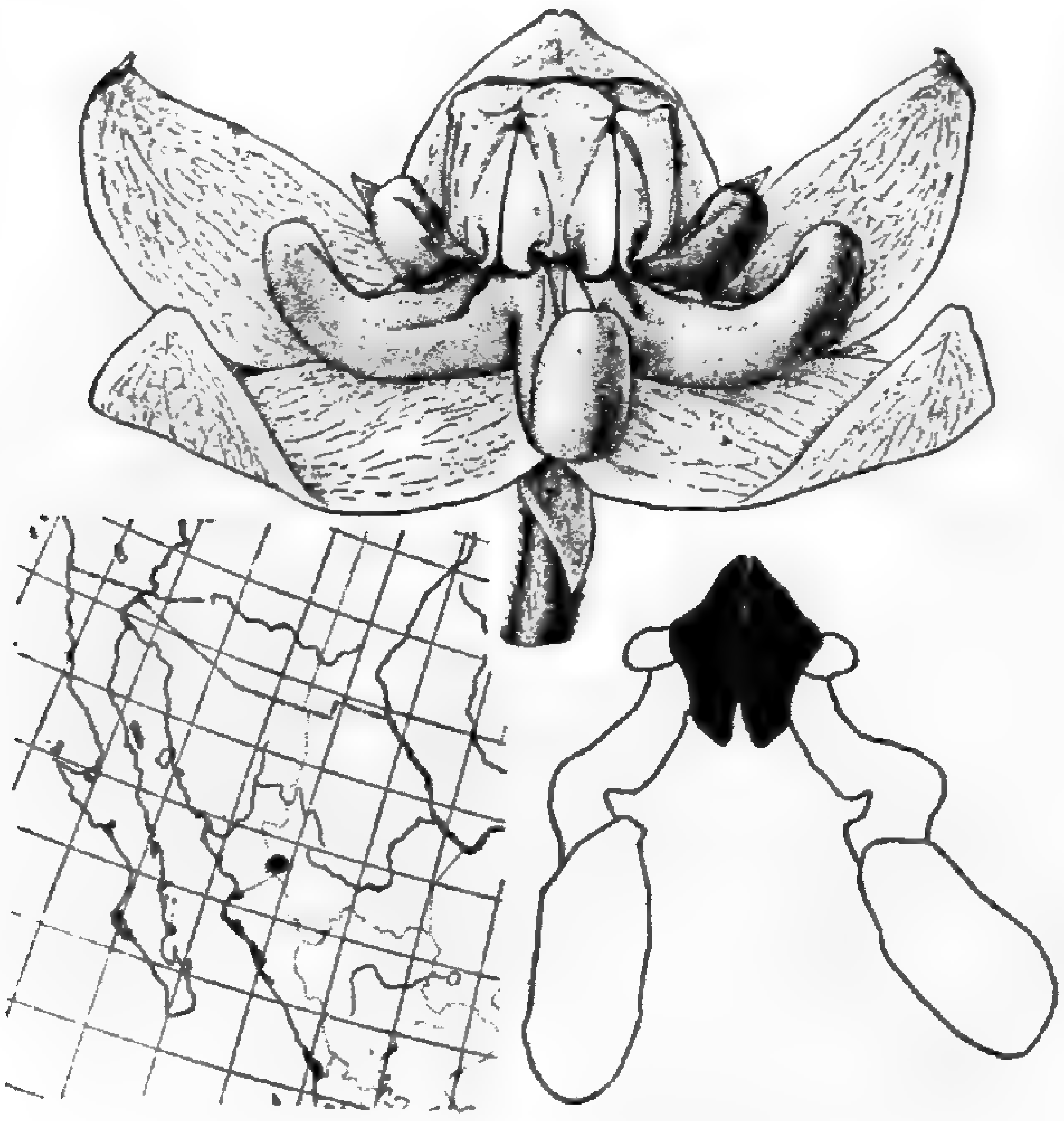

Fig. 105. *Asclepias mirifica* Woods.

the massive translator arms of the pollinia with their hyaline appendages so reminiscent of those of the latter species. If *A. mirifica* were represented by many sheets from a wide range, I would probably classify *A. elata* as a hybrid swarm between *A. mirifica* and *A. glaucescens!*

100. ASCLEPIAS FOURNIERI Woodson, in Ann. Missouri Bot. Gard. 28:207. [April 28] 1941. [Based on *Acerates gomphocarpoides* Dcne.]

Acerates gomphocarpoides Dcne. in Ann. Sci. Nat. Ser. II, 9:323. 1838, non *Asclepias gomphocarpoides* Schltr. [T.: *Andrieux 235*, P!]
Asclepiodora gomphocarpoides (Dcne.) Fourn. loc. cit. Ser. VI, 14:1882.
Gomphocarpus palmeri A. Gray, in Proc. Amer. Acad. 22:436. 1887, non *Asclepias palmeri* Vail. [T.: *E. Palmer 21*, GH!]
Blepharodon gomphocarpoides (Dcne.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4^2:243. 1895.
Asclepias grayi L. Benson, in Amer. Jour. Bot. 28:363. [June 4] 1941. [Based on *Gomphocarpus palmeri* A. Gray.]

Low herbaceous perennials from a tuberous subfusiform rootstalk. Stems relatively slender, simple or branching rather frequently, 6–30 cm. tall, minutely and densely puberulent. Leaves opposite, sessile, linear, 4–15 cm. long, 3–6 mm. broad, membranaceous, minutely tomentulose particularly beneath, glabrate above. Inflorescences subterminal and lateral from few to several of the uppermost nodes, few- to several-flowered, pedunculate; peduncles rather slender, 5–7 cm. long, minutely puberulent; pedicels very slender, about 1 cm. long, minutely puberulent. Flowers mediocre; calyx lobes ovate-lanceolate, very minutely puberulent; corolla rotate, reddish purple, somewhat puberulent without, the lobes 5–7 mm. long; gynostegium sessile, reddish purple, the hoods strongly deflexed from the anther head but with conspicuously ascending oblong tips about as long as the anther head, about 5 mm. long, the anther head truncate-conic, about 2 mm. long and 3 mm. broad. Follicles erect on deflexed pedicels, very narrowly fusiform, gradually attenuate, 8–10 cm. long, about 5 mm. thick, minutely puberulent to glabrate; seeds unknown.

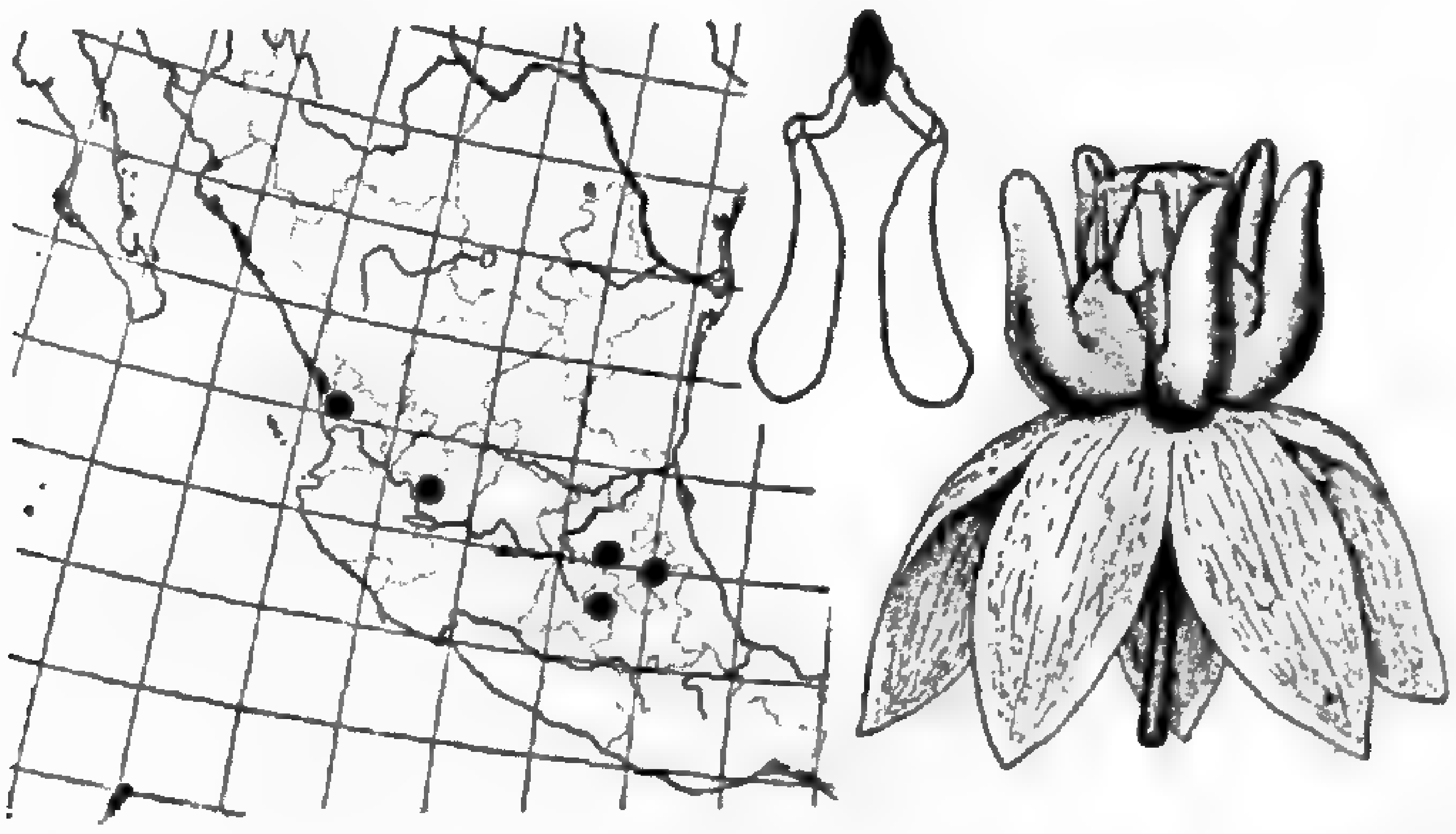
Fig. 106. *Asclepias fournieri* Woods.

Dry hillsides. Hidalgo and Mexico westward to Jalisco. Blooming from April to August.

MEXICO: HIDALGO: Huasca. JALISCO: Río Blanco, Guadalajara. MEXICO: Toluca, Ixtlahuaca. NAYARIT: Tepic.

101. ASCLEPIAS ZANTHODACRYON (L. B. Smith) Woodson, in Ann. Missouri Bot. Gard. 28:207. 1941.

Asclepiodora zanthodacryon L. B. Smith, in Contr. Gray Herb. no. 114:12. 1936. [T.: *Mueller & Mueller 816,* GH!]

Low herbaceous perennials from rather fusiform tuberous rootstalks. Stems rather slender, simple or branching from the caudex, 1–4 dm. tall, minutely pilosulose. Leaves opposite, sessile or subsessile, linear to linear-lanceolate, 4–15 cm. long, 1.5–4.0 mm. broad, membranaceous, very sparsely and minutely pilosulose to essentially glabrous. Inflorescences subterminal and solitary or also lateral from few of the uppermost nodes, few- to several-flowered, pedunculate; peduncles rather slender, 3–5 cm. long, minutely pilosulose; pedicels slender, 1.0–1.5 cm. long, minutely and densely puberulent. Flowers rather large; calyx lobes ovate-lanceolate, about 5 mm. long; corolla rotate, reddish purple or violet, the lobes 1.0–1.2 cm. long; gynostegium sessile, yellowish or pinkish cream, the hoods reduced to the broad, deflexed base, about 5 mm. long, the crest indefinite, the anther head very broadly subcylindric, about 2 mm. long and 3 mm. broad. Follicles unknown.

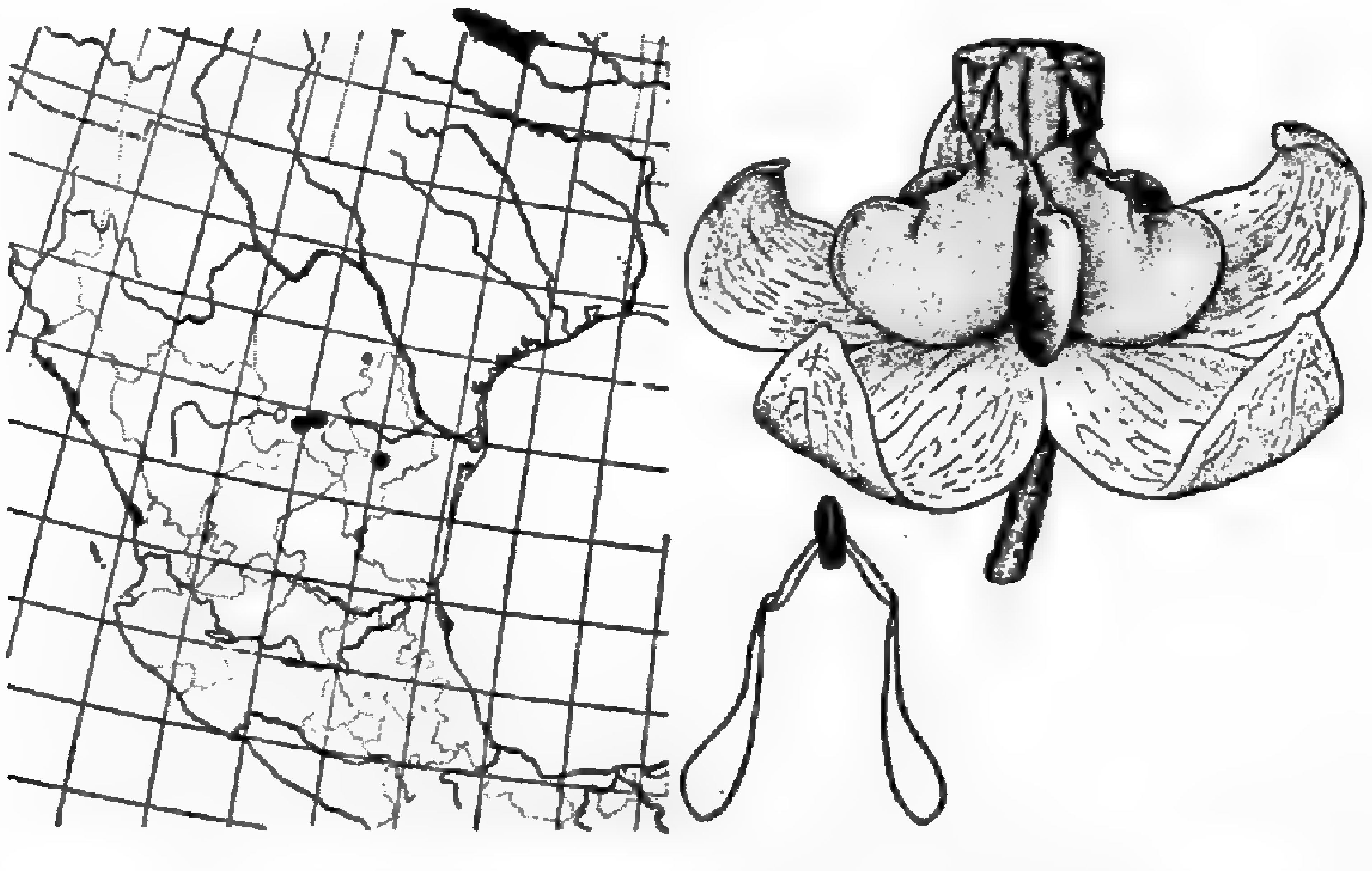

Fig. 107. *Asclepias zanthodacryon* (L. B. Smith) Woods.

Hillsides in pine or oak woods. Nuevo Leon and Coahuila. Blooming from May to July.

MEXICO: COAHUILA: Sierra de Parras. NUEVO LEÓN: Galeana.

102. ASCLEPIAS SPERRYI Woodson, in Ann. Missouri Bot. Gard. 28:246, *fig. 2.* 1841. [T.: *Sperry T553,* MO!]

Low suffruticose perennials. Stems clustered from the rootstalk and branching repeatedly and rather fastigiately, very slender, 1–3 dm. tall, very minutely puberulent to essentially glabrous. Leaves opposite, sessile, filiform, 6–8 cm. long, about 1 mm. broad, revolute, glabrous. Inflorescences lateral at few of the uppermost nodes, sessile, 1- (or very rarely 2-) flowered; pedicels filiform, about 5 mm. long, glabrous. Flowers rather small; calyx lobes ovate, about 2 mm. long; corolla rotate, pale greenish yellow more or less tinged with purple without, the lobes about 5 mm. long; gynostegium sessile, pale greenish yellow or white occasionally somewhat tinted with purple, the hoods tubiform, about 4 mm. long, the base abruptly deflexed from the anther head thence with ascending broadly expanded tips, the crest wholly adnate, low, the anther head very broadly cylindric, about 1 mm. long and 2.5 mm. broad. Follicles erect on deflexed pedicels, very narrowly fusiform, gradually attenuate, 5–7 cm. long, about 4 mm. thick, smooth, glabrous; seeds oval, about 5 mm. long, the white coma about 2.5 cm. long.

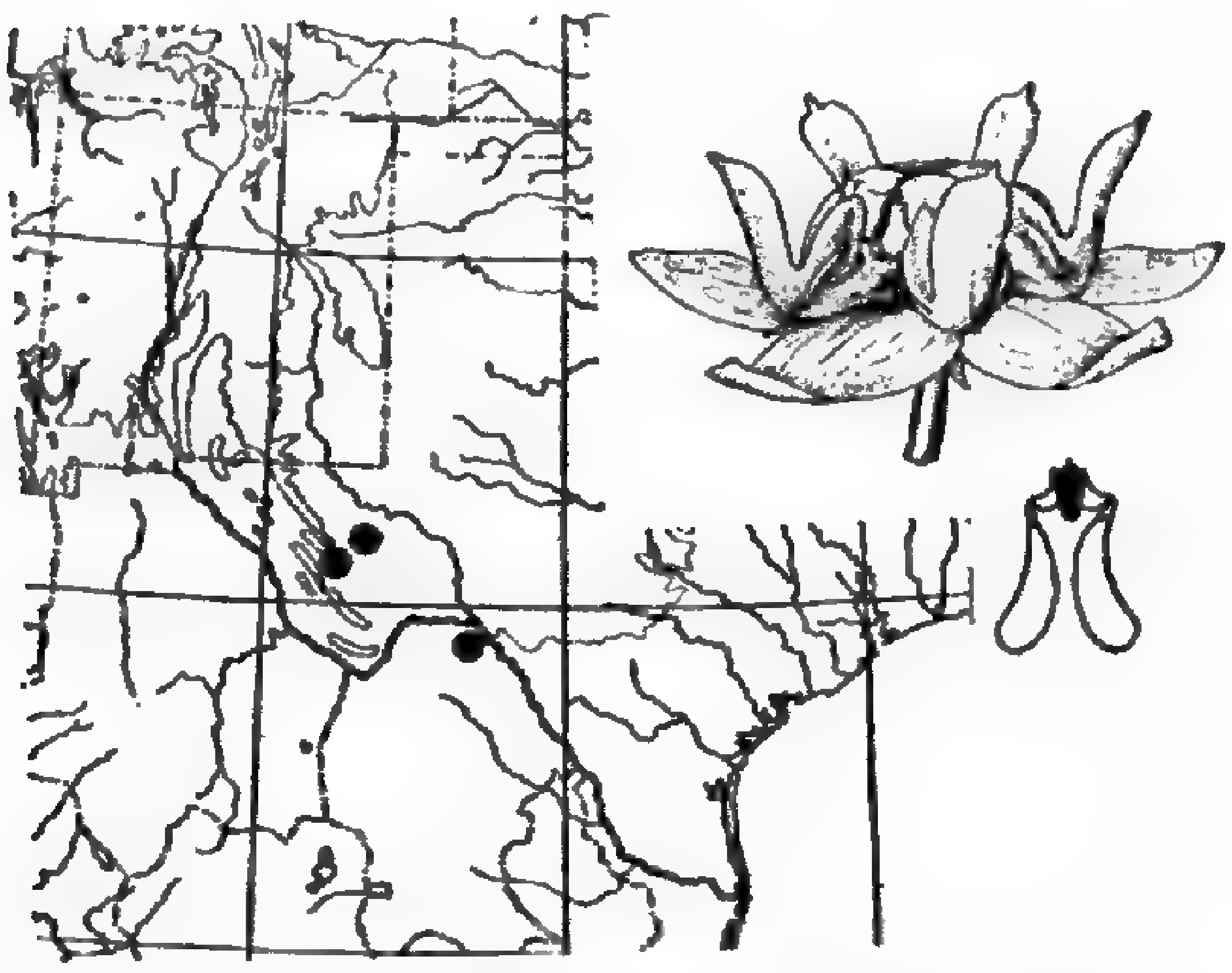

Fig. 108. *Asclepias sperryi* Woods.

Limestone ledges and slopes, open places among grass. Southwestern Texas; northern Coahuila. Blooming from April to August.

United States:
texas: Brewster and Pecos counties.
mexico: coahuila: Municipio de Villa Acuña, near Santo Domingo.

One of the oddest of American milkweeds not only because of the peculiar floral structure, but because of the extreme reduction of the inflorescence. The record from Coahuila is based upon a mixed collection, *Wynd & Muller 464*, which was distributed as *Dalea aurea* Nutt. Two sheets of this number in the herbarium of the University of Illinois are *Asclepias sperryi* and I have given to them the number *464a*. Dr. C. H. Muller informs me that the milkweeds were collected in Coahuila without doubt, and probably at the same place and date as the *Dalea*.

103. Asclepias viridis Walt. Fl. Carol. 107. 1788, ex char.

Anthanotis viridis (Walt.) Raf. Fl. Ludov. 52. 1817.
Asclepias procumbens Raf. loc. cit. 51. 1817, ex char.
Anthanotis procumbens (Raf.) Raf. loc. cit. 1817.
Anantherix viridis (Walt.) Nutt. Gen. North Amer. Pl. 1:169. 1818.
Podostigma viridis (Walt.) Ell. Sketch Bot. S. Car. & Ga. 1:327. 1821.
Gomphocarpus viridis (Walt.) Spreng. Syst. 1:849. 1825.
Anantherix ovata Raf. Atl. Jour. 146. 1832, ex char.
Anantherix paniculata Nutt. in Trans. Amer. Phil. Soc. 5:203. 1837, ex char. [T.: *Nuttall s. n.*]
Anantherix grandiflora Raf. New Fl. North Amer. 4:59. 1838, ex char.
Anantherix torreyana G. Don, Gen. Syst. 4:146. 1838. [Based on *Asclepias viridis* Walt.]
Acerates paniculata (Nutt.) Dcne. in DC. Prodr. 8:521. 1844.
Asclepias longipetala Scheele, in Linnaea 21:757. 1848. [T.: *Lindheimer 345*, MO!]
Asclepiodora viridis (Walt.) A. Gray, in Proc. Amer. Acad. 12:66. 1877.

Low herbaceous perennials from a stout, subfusiform rootstalk. Stems erect, ascending, or more or less decumbent. Stems usually simple or branched from the caudex, rather stout, 1.5–6.0 dm. tall, essentially glabrous. Leaves irregularly

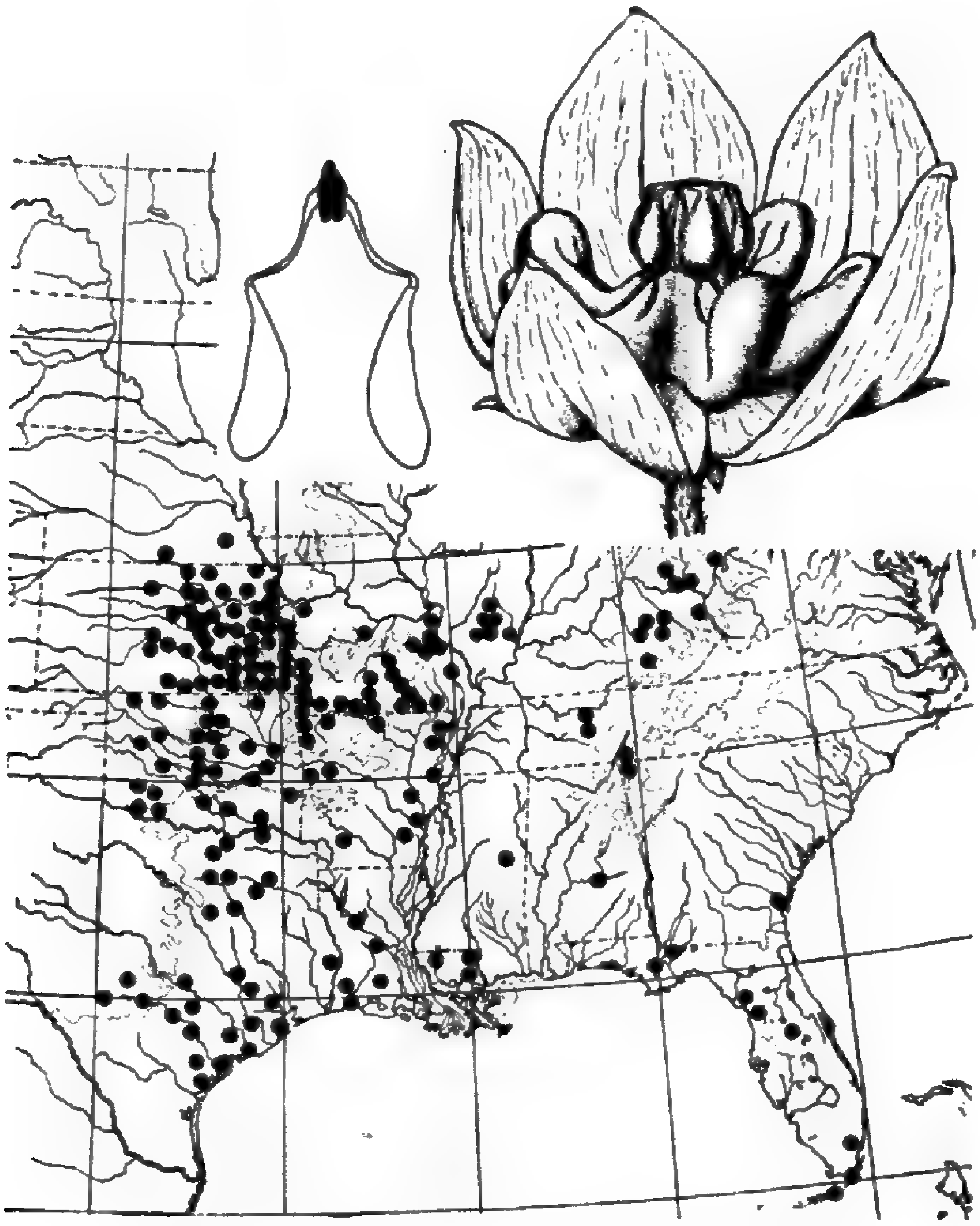

Fig. 109. *Asclepias viridis* Walt.

approximate, shortly petiolate, ovate to oblong-lanceolate, apex shortly acute to obtuse, base acute to broadly rounded, 4–13 cm. long, 1–6 cm. broad, firmly membranaceous, yellowish green, essentially glabrous; petioles 3–10 mm. long. Inflorescences terminal and solitary or more usually also lateral at few to several of the uppermost nodes, several- to many-flowered, crowded, pedunculate; peduncles 3–6 cm. long, minutely and scatteringly puberulent; pedicels rather slender, 1–3 cm. long, very minutely and sparsely puberulent. Flowers large and rather showy; calyx lobes lanceolate, 4–5 mm. long, essentially glabrous; corolla rotate, pale green, the lobes 1.3–1.5 cm. long, usually with ascending tips; gynostegium sessile, pale purplish rose, the hoods abruptly deflexed from the anther head and with rather shortly ascending rounded clavate tips, 4–6 mm. long, the anther head broadly truncate-conic, about 2 mm. long and broad. Follicles erect on deflexed pedicels, broadly fusiform to ovoid, greatly inflated, shortly apiculate, 6–13 cm. long, 2–3 cm. broad, minutely puberulent to glabrate; seeds oval, about 7 mm. long, the white or pale tawny coma about 4 cm. long.

Glades, prairies, dry hillsides, and dry pine barrens. Tennessee to Florida and westward to Nebraska and eastern Texas. Blooming from April to August.

United States:

alabama: Montgomery County.

arkansas: Arkansas, Baxter, Carroll, Craighead, Drew, Logan, Nevada, Poinsett, Prairie, St. Francis, Sebastian, and Washington counties.

florida: Citrus, Dade, Gadsden, Lake, Levy, Liberty, and Monroe counties.

GEORGIA: Dade and Glynn counties.

ILLINOIS: Bond, Clay, Clinton, Fayette, Marion, Perry, Richland, and Washington counties.

KANSAS: Anderson, Atchison, Barber, Bourbon, Brown, Butler, Cherokee, Chautauqua, Cloud, Coffey, Cowley, Crawford, Dickinson, Douglas, Edwards, Elk, Ellsworth, Franklin, Geary, Greenwood, Harper, Harvey, Jackson, Jefferson, Labette, Linn, Lyon, McPherson, Marshall, Miami, Montgomery, Morris, Neosho, Osage, Osborne, Pawnee, Pottawatomie, Reno, Riley, Saline, Sedgwick, Shawnee, Stafford, Sumner, Wabaunsee, Washington, Wilson, and Woodson counties.

KENTUCKY: Bath, Fayette, Jessamine, Lawrence, Powell, and Rockcastle counties.

LOUISIANA: Acadia, Calcasieu, Cameron, East Feliciana, Natchitoches, Rapides, St. Tammany, and Washington counties.

MISSISSIPPI: Oktibbeha County.

MISSOURI: Barry, Bates, Cass, Christian, Dallas, Dent, Franklin, Howell, Jackson, Jefferson, Jasper, Miller, Moniteau, Ozark, Ste. Genevieve, St. Francois, St. Louis, Taney, and Washington counties.

NEBRASKA: Lancaster and Webster counties.

OHIO: Adams, Highlands, Meigs, and Scioto counties.

OKLAHOMA: Alfalfa, Blaine, Caddo, Cherokee, Choctaw, Cleveland, Comanche, Cotton, Johnson, Kay, Kiowa, Le Flore, Lincoln, Logan, McClain, Murray, Muskogee, Noble, Nowata, Oklahoma, Pawnee, Payne, Pittsburgh, Pottawatomie, Tillman, Tulsa, and Washington counties.

TENNESSEE: Hamilton, Rutherford, and Wilson counties.

TEXAS: Arkansas, Burleson, Caldwell, Calhoun, Collin, Comal, Dallas, Galveston, Gillespie, Grayson, Hays, Harris, Hill, Jackson, Johnson, Kendall, Kerr, Lamar, Matagorda, Navarro, Newton, Refugio, Tarrant, Travis, Van Zandt, Washington, Wharton, and Wood counties.

Local populations of *A. viridis* frequently show distinctive variations of leaf size and outline, but on the whole the species is remarkably constant.

104. ASCLEPIAS **asperula** (Dcne.) Woodson, comb. nov.

Acerates asperula Dcne. in DC. Prodr. 8:522. 1844. [T.: *Ghiesbreght s. n.*, P!]
Asclepiodora asperula (Dcne.) Fourn. in Ann. Sci. Nat. Bot. Ser. VI, 14:369. 1882.

Low herbaceous perennials from very stout rootstalks. Stems usually clustered from the rootstalk, ascending or somewhat decumbent, simple, rather stout, 2–6 dm. tall, minutely and rather roughly pilosulose. Leaves irregularly approximate, shortly petiolate, lanceolate to linear-lanceolate, narrowly acuminate, base acute to obtuse, 10–20 cm. long, 1–3 cm. broad, firmly membranaceous, usually more or less conduplicate, minutely and usually rather sparsely pilosulose; petioles 3–7 mm. long. Inflorescences terminal and solitary, usually many-flowered and very crowded, sessile to long-pedunculate; peduncles obsolete to 10 cm. long, minutely and rather sparsely pilosulose, rather stout; pedicels more slender, 1.5–2.5 cm. long, minutely tomentulose. Flowers rather large; calyx lobes ovate to ovate-lanceolate, 4–5 mm. long, minutely pilosulose or puberulent; corolla rotate, pale yellowish green sometimes slightly flushed with purple without, the lobes 9–12 mm. long; gynostegium sessile, the hoods broadly clavate-falciform, abruptly deflexed from the anther head thence with ascending bluntish but tapering tips, 8–10 mm. long, greenish cream to rather dark purple, the anther head very depressed, about 2 mm. long and 5 mm. broad. Follicles erect on deflexed pedicels, rather narrowly fusiform, gradually attenuate, 4–13 cm. long, 1.0–2.5 cm. thick, smooth, minutely pilosulose; seeds oval, 7–8 mm. long, the pale tawny coma about 3 cm. long.

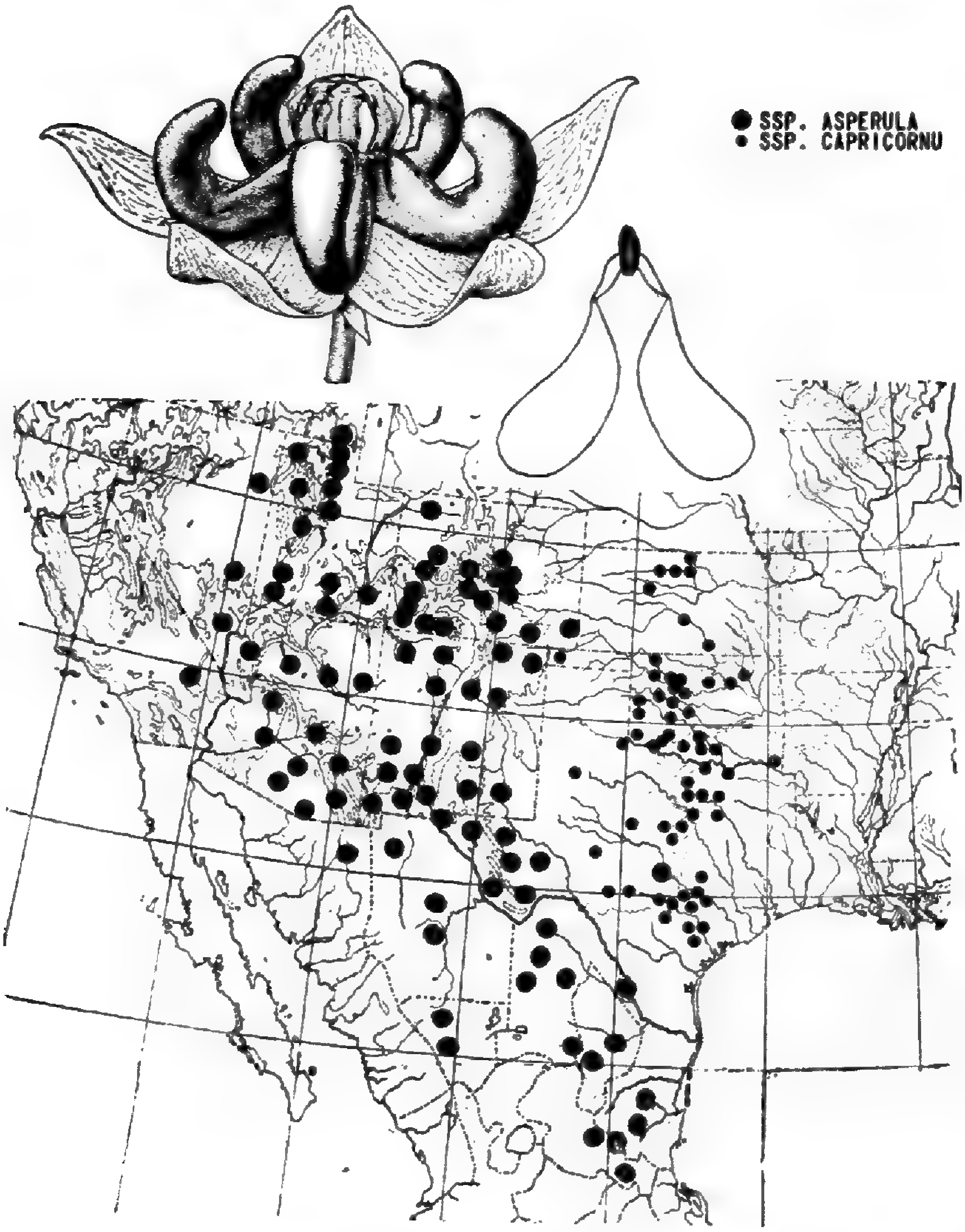

Fig. 110. *Asclepias asperula* (Dcne.) Woods.

KEY TO THE SUBSPECIES

Inflorescences usually obviously and rather long-pedunculate; hoods usually rather dark purple; leaves usually linear-lanceolate. Colorado and western Texas to Utah, Arizona, Nevada, and adjacent Idaho and California; Tamaulipas westward to Sonora and southward to San Luis Potosí and Hidalgo .... 104a. *A. asperula asperula*

Inflorescences sessile or subsessile; hoods usually greenish cream; leaves usually more broadly lanceolate. Eastern and central Oklahoma, Texas, and southern Kansas..104b. *A. asperula capricornu*

Asclepias asperula is an obviously necessary correction for my *A. capricornu* ignorantly proposed some years ago. It appears to me that the center of distribution for the species is in northern Mexico, from whence two divergent lines have advanced to the north and northeast respectively, representing the extremes of the two subspecies. At first one might question whether *A. asperula capricornu* might owe its existence to occasional hybridization with *A. viridis,* with which it is frequently associated geographically and ecologically, since its general appearance frequently is somewhat suggestive of the latter. However, there is never any question of the identity of the two species, and I believe that they do not hybridize in nature.

104a. ASCLEPIAS ASPERULA ssp. ASPERULA.

Asclepias capricornu ssp. *occidentalis* Woodson, in Ann. Missouri Bot. Gard. 32:371. 1945. [T.: *Clokey 8613*, MO!]

Flats and desert swales, sandy and rocky hillsides, with pinyon and juniper, oak, mesquite, *Yucca* and *Nolina*. Colorado and western Texas to Utah, Arizona, Nevada, and adjacent Idaho and California; Tamaulipas westward to Sonora and southward to Hidalgo and San Luis Potosí. Blooming from March to August.

UNITED STATES:

ARIZONA: Apache, Cochise, Coconino, Gila, Graham, Maricopa, Mohave, Pima, Pinal, Santa Cruz, and Yavapai counties.

CALIFORNIA: San Bernardino County.

COLORADO: Archuleta, Baca, Boulder, Chaffee, Denver, El Paso, Fremont, Garfield, Huerfano, Jefferson, Lake, La Plata, Las Animas, Moffat, Montezuma, Montrose, Prowers, San Miguel, and Teller counties.

IDAHO: Franklin County.

NEVADA: Clark, Elko, and Lincoln counties.

NEW MEXICO: Catron, Colfax, Dona Ana, Eddy, Grant, Hidalgo, Lincoln, Luna, Otero, Rio Arriba, Sandoval, San Juan, San Miguel, Santa Fe, Sierra, Socorro, and Union counties.

TEXAS: Brewster, Culberson, El Paso, Hudspeth, Jeff Davis, Llano, Pecos, and Presidio counties.

UTAH: Box Elder, Cache, Garfield, Iron, Juab, Kane, Salt Lake, San Juan, Tooele, Utah, Washington, and Weber counties.

MEXICO: CHIHUAHUA: Chihuahua, Santa Eulalia Mtns. COAHUILA: Múzquiz, Cuesta Zozaya, Del Carmen Mtns., Sierra Mojada Mtns., Monclova, Sierra de San Miguel, Saltillo. DURANGO: Ramos, Inde, Tepehuanes. HIDALGO: Jacala. NUEVO LEÓN: Monterrey, Nuevo Laredo, Sierra La Silla, Puerta. SAN LUIS POTOSÍ: Sierra Tablón, Minas de San Rafael, Rascón. SONORA: Sierra Madre. TAMAULIPAS: Jaumave, Victoria.

104b. ASCLEPIAS ASPERULA ssp. **capricornu** (Woodson) Woodson, stat. nov.

Anantherix angustifolia Raf. Atl. Jour. 146. 1832, nec *Asclepias angustifolia* Schweigg. nec alior., ex char.

Anantherix decumbens Nutt. in Trans. Amer. Phil. Soc. 5:203, 1837, non *Asclepias decumbens* L. [T.: *Nuttall s. n.*, MO, photo!]

Anantherix nuttalliana G. Don, Gen. Syst. 4:146. 1838, non *Asclepias nuttalliana* nec A. Gray nec Torr. [Based on *Anantherix decumbens* Nutt.]

Acerates decumbens (Nutt.) Dcne. in DC. Prodr. 8:522. 1844.

Asclepiodora decumbens (Nutt.) A. Gray, in Proc. Amer. Acad. 12:67. 1877.

Asclepias decumbens (Nutt.) K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. 4^2:239. 1895, non L.

Asclepias capricornu Woodson, in Ann. Missouri Bot. Gard. 32:370. 1945. [Based on *Anantherix decumbens* Nutt.]

The best nomenclatural procedure here is not entirely clear to me, but it seems preferable to attempt to salvage the name *capricornu*.

Prairies, plains, limestone, sandstone, or clay hills; spreading to pastures. Eastern and central Oklahoma and Texas, southern Kansas. Blooming from March to July.

UNITED STATES:

KANSAS: Cowley, Ellis, Jewell, Mitchell, Osborne, Reno, and Rooks counties.

OKLAHOMA: Beckham, Blaine, Caddo, Carter, Cimarron, Cleveland, Comanche, Custer, Greer, Harmon, Johnston, Kingfisher, McClain, McCurtain, Murray, Oklahoma, Payne, Pottawatomie, Roger Mills, Rogers, Stephens, Tillman, Tulsa, Woodward, and Woods counties.

TEXAS: Bastrop, Bexar, Caldwell, Childress, Comal, Comanche, Cooke, Dallas, De Witt, Eastland, Edwards, Ellis, Erath, Goliad, Grayson, Hays, Hood, Irion, Karnes, Kendall, Kerr, Lubbock, Parker, Tarrant, Taylor, Travis, Williamson, and Wise counties.

SUBGENUS IX. PODOSTIGMA (Ell.) Woodson, stat. nov.

Podostigma Ell. Sketch Bot. S. Car. & Ga. 1:326. 1821. [T.: *P. pubescens* Ell.]

KEY TO THE SPECIES

a. Corolla rotate-campanulate, the lobes broadly ascending, purple or rose; anther head stipe shorter than the hoods.
  b. Anther head about as long as broad; flowers relatively small, the corolla lobes somewhat longer than 1 cm.; leaves opposite, linear or the lowermost elliptic-lanceolate. Mexico southward to Guerrero and Oaxaca .... 105. *A. circinalis*
  bb. Anther head broader than long.
    c. Flowers relatively large, the corolla lobes somewhat longer than 1 cm.; leaves linear to filiform, those of the middle stem congested into false whorls of 4. Jalisco........ 106. *A. mcvaughii*
    cc. Flowers relatively small, the corolla lobes somewhat shorter than 1 cm.; leaves linear, opposite. Durango .... 107. *A. atroviolacea*
aa. Corolla rotate-tubular, the lobes erect, greenish cream; anther head stipe much longer than the hoods. Coastal Plain: southern North Carolina to Florida........ 108. *A. pedicellata*

I had long thought *Podostigma* to be the most distinct of the numerous North American segregates of *Asclepias,* because of the very unusual flowers of the single species, *P. pedicellata.* However, *Asclepias circinalis* and *A. atroviolacea,* so clearly related to *Asclepiodora,* completely close the morphological gap between the two segregates. I am of the opinion that the three species of subgen. PODOSTIGMA according to my treatment certainly are not lineally related and that *A. pedicellata* still stands apart, but the opinion is intuitive only.

105. ASCLEPIAS CIRCINALIS (Dcne.) Woodson, in Ann. Missouri Bot. Gard. 28:207. 1941.

Acerates circinalis Dcne. in Ann. Sci. Nat. Ser. II, 9:322, *t. 11 f. c.* 1838. [T.: *Andrieux 238,* P!]
Asclepiodora circinalis (Dcne.) Fourn. loc. cit. Ser. VI, 14:369. 1882.

Low herbaceous perennials from a fleshy fusiform rootstalk. Stems slender, simple or branching from the caudex, 5–15 cm. tall, very minutely and rather sparsely puberulent, usually dark reddish. Leaves opposite, sessile, linear, 5–13 cm. long, 2–4 mm. broad, membranaceous, revolute, very inconspicuously and sparsely pilosulose. Inflorescences terminal and usually lateral from a few of the uppermost nodes, subsessile or very shortly pedunculate, few- to several-flowered; peduncles slender, obsolete to about 2 cm. long; pedicels very slender, 1–2 cm. long, very inconspicuously pilosulose. Flowers large; calyx lobes narrowly lanceolate, about 3 mm. long, dark purple, very inconspicuously and sparsely pilosulose. Corolla rotate-campanulate, purplish rose, the lobes 1.0–1.5 cm. long; gynostegium sessile but produced into a rather stout stipe about 3 mm. long immediately beneath the anther head, paler rose-purple, the hoods suberect, subfalciform-clavate, 5–6 mm. long, the adnate crest broadly rounded and rather prominent, the anther head about 3 mm. long and broad. Follicles erect on deflexed pedicels, narrowly fusi-

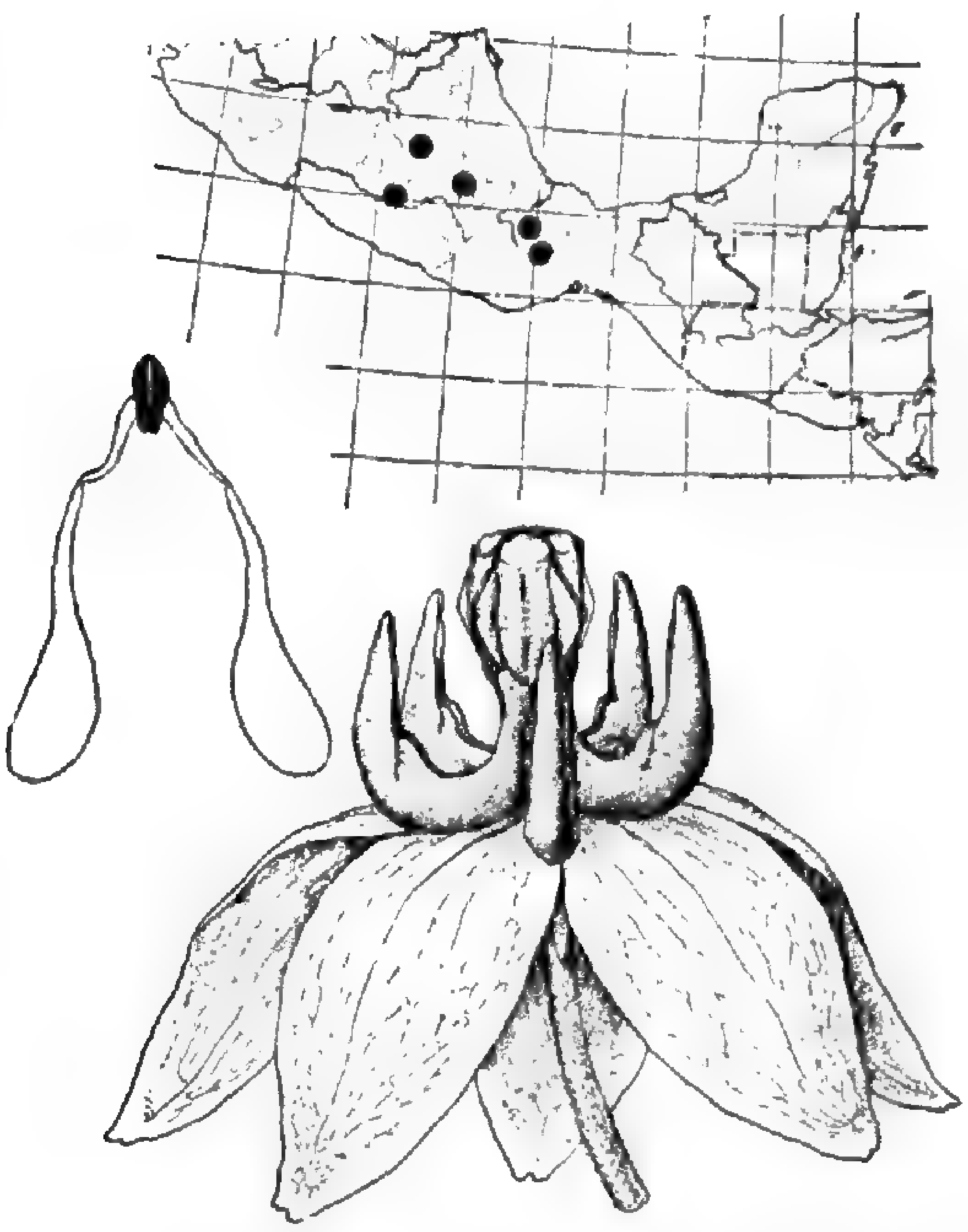

Fig. 111. *Asclepias circinalis* (Dcne.) Woods.

form, long-attenuate, 9–10 cm. long, about 1 cm. broad, sparsely and inconspicuously pilosulose; seeds oval, about 6 mm. long, the pale tawny coma about 4 cm. long.

Dry oak and pine woods. Mexico southward to Guerrero and Oaxaca. Blooming from January to September.

Mexico: GUERRERO: Mina. MEXICO: Temascaltepec. OAXACA: Sierra de San Felipe, Sierra de Ixtlan, San Pedro Yolox. PUEBLA: Caxcatlan.

106. Asclepias **mcvaughii** Woodson, spec. nov.

Herbae perennes tenues e rhizomate crasso fusiformi. Caules graciles erecti simplices 3–6 dm. alti inconspicue puberuli. Folia linearia vel filiformia inferiora superioraque opposita caeteraque in medio caulis per congestionem nodium false quaternata sessilia 4.5–12.0 cm. longa 1–4 mm. lata membranacea revoluta sat glabra. Inflorescentiae 1–5 in nodis summis laterales pauciflorae; pedunculis ca. 1.5 cm. longis in fructu accrescentibus; pedicellis gracilibus ca. 1 cm. longis. Flores sat magni; calycis laciniis ovato-lanceolatis ca. 3 mm. longis. Corolla rotato-campanulata rosea, lobis ca. 1.2 cm. longis; gynostegio sessili sed sub androecio in stipitem truncate conicum ca. 3 mm. longum producto pallidius roseo, cucullis ascendentibus falciformi-clavatis apicibus attenuatis patulis ca. 5 mm. longis, androecio depresso ca. 1.5 mm. alto 4.5 mm. lato. Folliculi erecti pedicellis reflexis anguste fusiformes 8–9 cm. longi 6–7 mm. crassi laeves glabri, seminibus comosis. —Holotypus: *R. McVaugh 13800* in Herb. Univ. Michigan. (State of Jalisco, Mexico, Sierra de la Campana, along road to Mascota, 7–8 miles northwest of Los Volcanes, elevation 1900–2000 m.; pine oak forests west of summits, 23–25 October, 1952.)

The description of the fruits is taken from two specimens without flowers col-

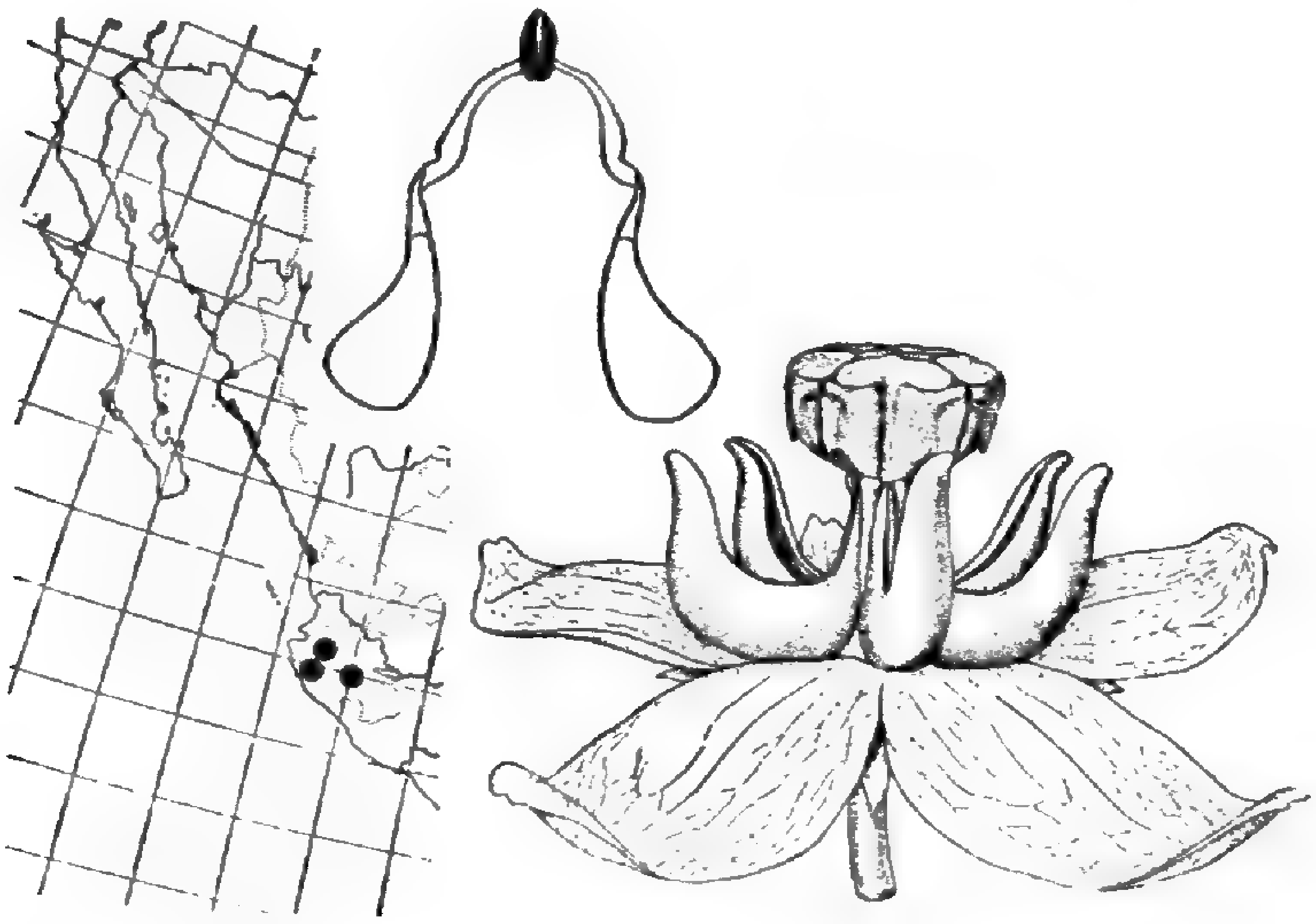

Fig. 112. *Asclepias mcvaughii* Woods.

lected in the same general vicinity by Dr. McVaugh: *McVaugh 14386* (Sierra de Cuale, southwest of Talpa de Allende; southwest of the prominent peak called Piedra Rajada; pine forests near summits, on steep south- and west-facing slopes, elevation 1800–2250 m., 19–21 November, 1952), and *McVaugh 13953* (Sierra de Manantlán, 15–20 miles southeast of Autlán, on the *bajada* south and west of the divide between Aserradero San Miguel Uno and Durazno, elevation ca. 1700 m.; steep west-facing slopes in pine forest, 7 November, 1952).

Asclepias mcvaughii obviously is very closely related to *A. atroviolacea*, with which I was familiar before I was sent the sheets of the former. In all three sheets of *A. mcvaughii* several of the middle leaf nodes are congested to form false whorls of quaternate leaves, reminiscent of *A. quadrifolia;* the flowers of the holotype are larger, more spreading, and paler than those of *A. atroviolacea*, and the hoods more conspicuously tapered. It may well be that the two species represent rather two complementary subspecific populations, but our scanty material does not justify this view at the moment. Dr. McVaugh comments that at the two localities where he collected fruit the plants are "occasional" and "frequent, but widely scattered", respectively.

107. Asclepias **atroviolacea** Woodson, spec. nov.

Herbae perennes tenues e rhizomate crasso fusiformi. Caules graciles erecti simplices 2–4 dm. alti minute appresse puberuli. Folia opposita aliquando ternata sessilia linearia 3–5 cm. longa ca. 3 mm. lata membranacea revoluta sparsissime minuteque pilosula. Inflorescentiae terminales et in nodo summo laterales pauciflorae brevissime pedunculatae; pedunculis 1–2 cm. longis vel minus; pedicellis gracilibus ca. 6 mm. longis minute appresso-puberulis. Flores mediocres; calycis laciniis ovato-lanceolatis ca. 3 mm. longis. Corolla rotato-campanulata saturate purpurea, lobis ca. 7 mm. longis; gynostegio sessili sed sub androecio in stipitem cylindricum ca. 3 mm. longum producto pallidius purpureo, cucullis ascendentibus late subfalciformi-clavatis ca. 5 mm. longis, androecio depresso ca. 2 mm. longo

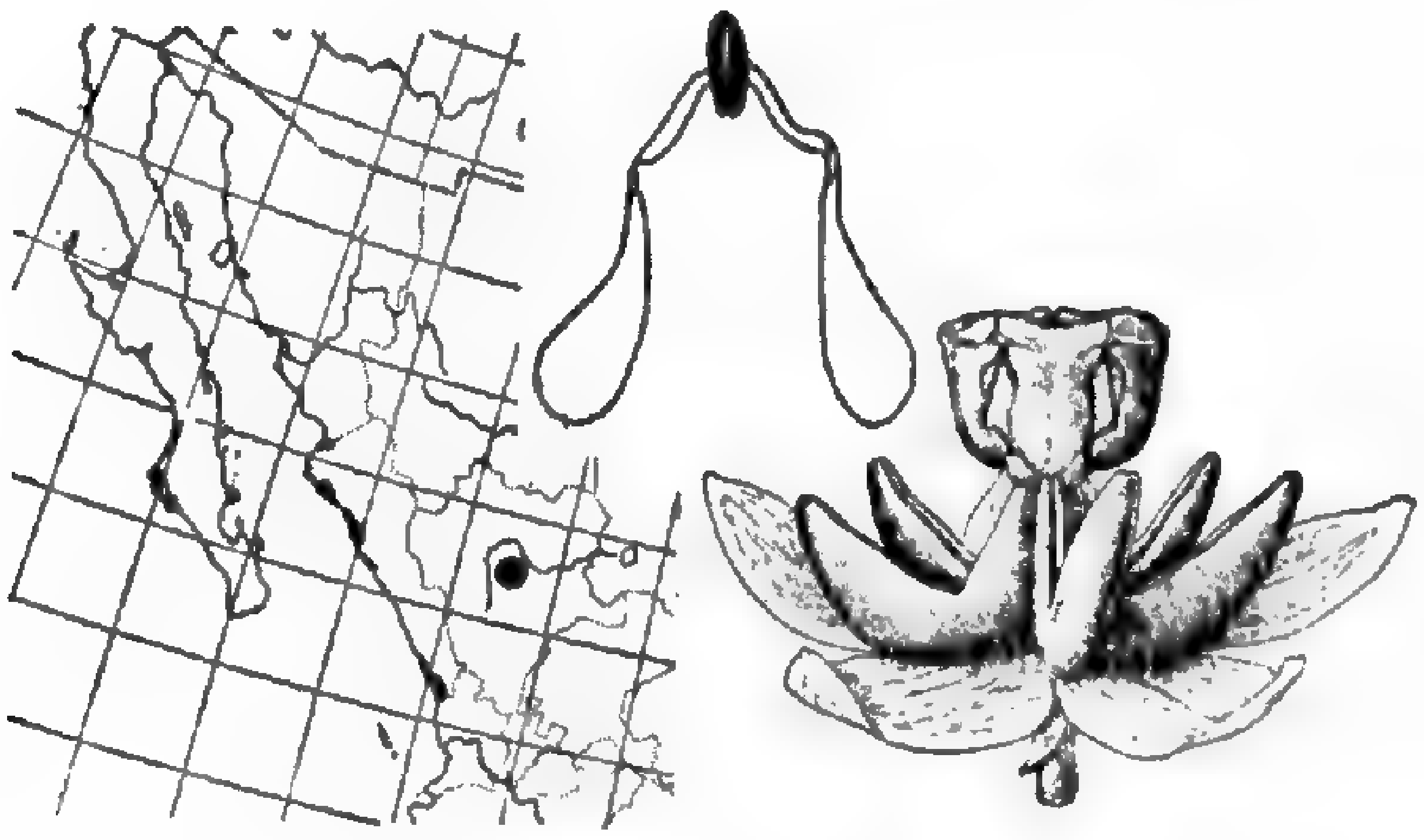

Fig. 113. *Asclepias atroviolacea* Woods.

4 mm. lato. Folliculi mihi ignoti.—Holotypus: *J. N. Rose 2250* in Herb. Missouri Bot. Gard., isotypus in Herb. U. S. Nat. Mus. (State of Durango, Mexico, locality lacking, August 13, 1897).

If this odd little plant had been collected in Florida, there would be no question of its close affinity with *A. pedicellata.* I feel that the development of the two species probably has been convergent rather than lineal, however.

108. Asclepias pedicellata Walt. Fl. Carol. 106. 1788, ex char.

Stylandra pumila Nutt. Gen. North Amer. Pl. 1:170. 1818. [T.: *Nuttall s. n.*, MO, photo!]
Anthanotis pedicellata (Walt.) Raf. Fl. Ludov. 52. 1817.
Podostigma pubescens Ell. Sketch Bot. S. Car. & Ga. 1:326. 1821, ex char.
Anantherix pumilus (Nutt.) Nutt. in Trans. Amer. Phil. Soc. 5:203. 1837.
Podostigma pedicellata (Walt.) Vail, ex Small, Fl. Southeast. U. S. 939. 1903.

Low herbaceous perennials from a tuberous fusiform rootstalk. Stems erect, slender, simple, 1–5 dm. tall, minutely and rather sparsely puberulent. Leaves opposite, sessile, linear to ovate-lanceolate, apex acuminate, base acute or obtuse, 2–5 cm. long, 3–10 mm. broad, firmly membranaceous, minutely and rather sparsely puberulent particularly beneath. Inflorescences terminal and lateral at the uppermost few nodes, few-flowered, shortly pedunculate; peduncle slender, 1.0–2.5 cm. long, minutely puberulent; pedicels very slender, about 1 cm. long, very minutely puberulent. Flowers rather mediocre; calyx lobes ovate, about 2 mm. long, essentially glabrous; corolla rotate-tubular, greenish cream, the lobes nearly erect, nearly 1 cm. long; gynostegium sessile but produced into a rather slender stipe about 5 mm. long, directly beneath the anther head, the hoods erect, subampulliform, about 3 mm. long, the

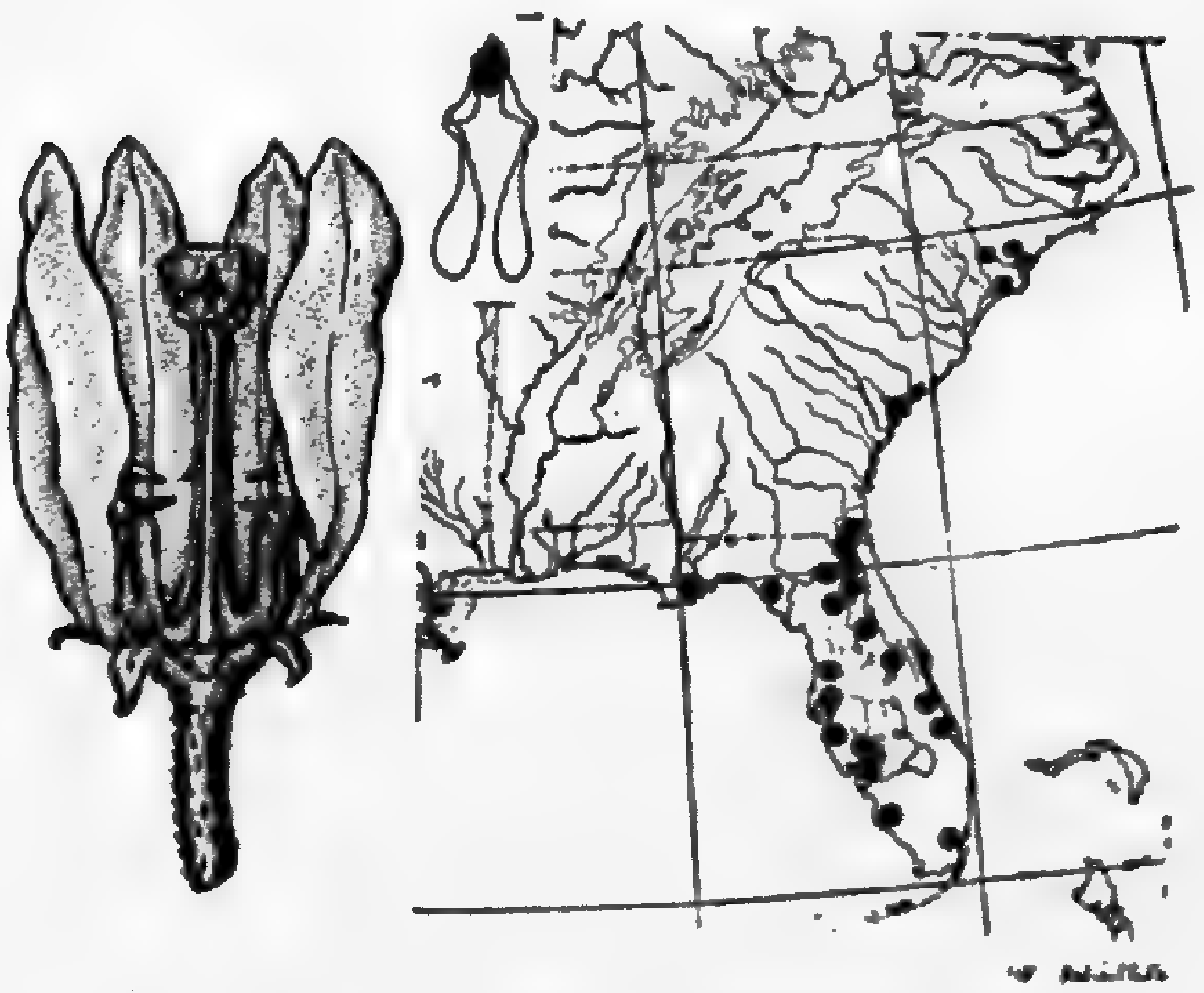

Fig. 114. *Asclepias pedicellata* Walt.

anther head depressed-obconic, about 1 mm. long and 2 mm. broad. Follicles unknown.

Pine barrens and flatwoods. Florida and coastal Georgia, South Carolina and North Carolina. Blooming from May to June.

United States:

florida: Alachua, Brevard, Charlotte, Clay, Collier, Dade, De Soto, Dixie, Duval, Franklin, Hernando, Hillsborough, Lake, Manatee, Marion, Nassau, Orange, Putnam, and St. Lucie counties.

georgia: Charlton County.

north carolina: Bladen, Brunswick, New Hanover, and Pender counties.

south carolina: Beaufort County.

This artfully contrived little species is a far cry indeed from *Asclepias incarnata*, but connected to it through innumerable intergrading mutations amongst the intervening scores of species, as we have seen.

Enumeration of the Species

Subgenus I. Asclepias

Series 1. incarnatae

1\. *incarnata* L.
  1a. ssp. *incarnata*
  1b. ssp. *pulchra* (Ehrh.) Woods.
2\. *texana* Heller
3\. *perennis* Walt.
4\. *woodsoniana* Standl. & Steyerm.
5\. *linearis* Scheele
6\. *pseudorubricaulis* Woods.
7\. *curassavica* L.
8\. *nivea* L.
9\. *angustifolia* Schweig.
10\. *fascicularis* Dcne.
11\. *subverticillata* (A. Gray) Vail
12\. *mexicana* Cav.
13\. *verticillata* L.
14\. *pumila* (A. Gray) Vail
15\. *leptopus* I. M. Johnston
16\. *gentryi* Standl.

Series 2. tuberosae

17\. *tuberosa* L.
  17a. ssp. *tuberosa*
  17b. ssp. *rolfsii* (Britton) Woods.
  17c. ssp. *interior* Woods.
  17d. ssp. *terminalis* Woods.
18\. *rubra* L.
19\. *lanceolata* Walt.

Series 3. exaltatae

20\. *ovata* Mart. & Gal.
21\. *similis* Hemsl.
22\. *contrayerba* Sessé & Moc.
23\. *exaltata* L.
24\. *coulteri* A. Gray
25\. *quinquedentata* A. Gray
26\. *amplexicaulis* Sm.
27\. *virletii* Fourn.
28\. *scaposa* Vail

Series 4. grandiflorae

29\. *crocea* Woods.
30\. *grandiflora* Fourn.
31\. *glaucescens* HBK.

Series 5. syriacae

32\. *quadrifolia* Jacq.
33\. *viridula* Chapm.
34\. *pellucida* Fourn.
35\. *ovalifolia* Dcne.
36\. *syriaca* L.
37\. *humistrata* Walt.
38\. *meadii* Torr.
39\. *hypoleuca* (A. Gray) Woods.
40\. *pringlei* (Greenm.) Woods.
41\. *pratensis* Benth.
42\. *linaria* Cav.

Series 6. purpurascentes

43\. *sullivantii* Engelm.
44\. *variegata* L.
45\. *purpurascens* L.
46\. *hallii* A. Gray
47\. *lanuginosa* HBK.
48\. *curtissii* A. Gray
49\. *speciosa* Torr.
50\. *euphorbiaefolia* Engelm.

Series 7. Macrotides

51. *michauxii* Dcne.
52. *conzattii* Woods.
53. *involucrata* Engelm.
54. *macrosperma* Eastw.
55. *puberula* A. Gray
56. *macrotis* Torr.
57. *lemmoni* A. Gray
58. *laxiflora* (Benth.) Dcne.

Series 8. Roseae

59. *tomentosa* Ell.
60. *arenaria* Torr.
61. *latifolia* Raf.
62. *obovata* Ell.
63. *labriformis* M. E. Jones
64. *erosa* Torr.
65. *eriocarpa* Benth.
66. *masonii* Woods.
67. *subaphylla* Woods.
68. *albicans* S. Wats.
69. *vestita* H. & A.
    69a. ssp. *vestita*
    69b. ssp. *parishii* (Jeps.) Woods.
70. *nummularia* Torr.
71. *rosea* HBK.

Series 9. Fruticosae

72. *fruticosa* L.

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73. *auriculata* HBK.
74. *subulata* Dcne.
75. *nyctaginifolia* A. Gray
76. *oenotheroides* Cham. & Schlecht.
77. *emoryi* (Greene) Vail
78. *standleyi* Woods.

Subgenus III. Anantherix (Nutt.) Woods.

79. *connivens* Baldw.

Subgenus IV. Asclepiodella (Small) Woods.

80. *cinerea* Walt.
81. *feayi* Chapm.
82. *brachystephana* Engelm.
83. *ruthiae* Maguire
84. *cutleri* Woods.
85. *uncialis* Greene
86. *cordifolia* (Benth.) Jeps.

Subgenus V. Acerates (Ell.) Woods.

87. *vinosa* (Fourn.) Woods.
88. *hirtella* (Pennell) Woods.
89. *longifolia* Michx.
90. *viridiflora* Raf.
91. *nuttalliana* Torr.

Subgenus VI. Solanoa (Greene) Woods.

92. *californica* Greene
    92a. ssp. *californica*
    92b. ssp. *greenei* Woods.
93. *cryptoceras* S. Wats.
    93a. ssp. *cryptoceras*
    93b. ssp. *davisii* (Woods.) Woods.
94. *solanoana* Woods.

Subgenus VII. Polyotus (Nutt.) Woods.

95. *stenophylla* A. Gray
96. *rusbyi* (Vail) Woods.
97. *engelmanniana* Woods.

Subgenus VIII. Asclepiodora (A. Gray) Woods.

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99. *mirifica* Woods.
100. *fournieri* Woods.
101. *zanthodacryon* (L. B. Sm.) Woods.
102. *sperryi* Woods.
103. *viridis* Walt.
104. *asperula* (Dcne.) Woods.
    104a. ssp. *asperula*
    104b. ssp. *capricornu* (Woods.) Woods.

Subgenus IX. Podostigma (Ell.) Woods.

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106. *mcvaughii* Woods.
107. *atroviolacea* Woods.
108. *pedicellata* Walt.

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Systematic Index

Roman type indicates accepted, preëxisting names; *italics* indicates synonyms; **bold face** indicates novelties.

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MAIZE AND SORGHUM AS A MIXED CROP IN HONDURAS

EDGAR ANDERSON* AND LOUIS O. WILLIAMS**

Maize and sorghum are planted together but harvested at separate times over considerable areas in Central America. Although standard practice for certain types of climate and soils, it does not seem ever to have been referred to in print. The following account is based on our observations in the valley of the Río Yeguare in central Honduras at an altitude of 2400 feet. From personal observation we believe these practices to be more or less typical of wide areas in Honduras, Guatemala, and Nicaragua.

PREPARATION OF THE LAND

The land chosen for the field is usually a low tangle of thorny shrubs, principally *carbón (Mimosa tenuiflora)* with associated weeds and grasses. Field size will depend upon the resources of the individual farmer and the lay of the land. Some of the fields are as small as half an acre; others will be of ten to twenty acres or more. Fields prepared in this way would previously have been in more or less deserted pastures often thickly infested with *carbón*. Sometimes former fields will be burned over if the weed and brush cover is lush enough to produce a hot enough fire; otherwise the land would have to be cultivated before the crop was sown. Sometimes in the dry season the brush and weeds will be chopped down and left to dry. At the very beginning of the wet season this slash is burned. Planting is deferred until there has actually been a rain. The combination of the burning followed by rain produces a soil almost as mellow as if it had been cultivated.

PLANTING

The unburned brush is kicked and piled out of the way and the planting proceeds. Each man uses a planting stick: a strong pole higher than his head, shod at one end with a sharp metal blade. The metal head is home-made from such odds and ends of steel or iron as may be available and no two of them are exactly alike. Each man carries two seed pouches tied around his waist, one for maize and one for sorghum. Most commonly they are *jicaras* (*Crescentia alata* and *C. cujete,*

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calabash tree fruits) though rawhide pouches and various other containers are frequently used. It will be seen that one of the men in the illustration (pl. 5, fig. 1) is wearing one *jicara* and one square container fashioned out of a box of corrugated cardboard. The men start at one end of the field and proceed across it in approximately straight lines, planting the grain in hills of four or five plants each. The planting stick is held in one hand and is forced vigorously down into the earth to the depth of several inches (pl. 5, fig. 2). It is then pushed forward with the arm while with the other hand the grains are dropped into the hole formed by the levered planting stick. The stick is then pulled out and, with the foot, soil is scuffed over the hole and the earth is compacted. The operation in its results and in most of the actual motions employed is remarkably similar to the planting of experimental plots of maize with patented hand planters such as were used in the United States corn belt before the advent of power machinery.

Sorghum and maize are planted in paired but distinctly separate hills, as shown in pl. 6, fig. 2. A hill of one is planted, then the planting stick is inserted a few inches to the right or left and the other grain is planted. Then the operator moves on to the next spot and again plants paired hills, one of sorghum and one of maize, and proceeds in this way across the field.

Still other crops are often planted in the same fields. At higher elevations potatoes are sown in approximately straight lines between the grain hills, and it is common practice to plant squash here and there throughout the corn field.

The field is usually cultivated once, using a heavy iron hoe (something like the grub hoes of the United States) on a long handle (pl. 5, fig. 3). In Guatemala very wide and heavy hoes fully twice the width of these are commonly employed. Weeds and sprouts are cleared out with this implement when the maize is about waist high and the field is then left to shift for itself (much as in the United States corn belt where it is said to be "laid by" after the last cultivation). The maize ripens first (or fails altogether if there is not sufficient rain during the wet season). It is harvested when convenient. If it is harvested fairly early when scarcely ripe the husks are pulled back, and the ears, tied together in pairs, are hung over a rope or a rafter. It may be left until well ripened; it is then usually stored in a corn bin *(troja)* within the house or adjacent to it. One of the most careful cultivators makes a temporary wall at the end of the crib with neatly piled ears whose inner husks have been left on the ear. The remaining ears, completely husked, are thrown in back of this wall. Sometimes the maize is stored temporarily on the plant, the stalks being bent over sharply just below the ear. In this way moisture is kept out of the ripening ears and bird damage is reduced to a minimum.

The sorghum ripens much later, during the dry season. By the end of December, all the maize will have ripened; most of it will be harvested; and even in a good year, much of it will have been consumed, mostly as human food. By this time, the sorghum will have tasseled and will be rapidly maturing in the dry weather. It is harvested during the dry season and is used as a substitute for maize when that crop was not sufficient and as a stock food and chicken food. The grains of sorghum are frequently popped and made into "popcorn" balls *(alborotos)* though these may also be made from popcorn.

The interplanting of maize and sorghum thus distributes the labor and the harvest over a longer period and is particularly valuable in years when there is not sufficient rainfall to mature a good crop. To casual questioning the usual reply is that sorghum is raised for the chickens and maize for the family. Careful inquiry brings out the information that in bad years much of the sorghum is used as human food.

The maize grown in the valley of the Yeguare, and in similar areas near by, is of a fairly well-marked type. It is prevailingly white (yellow becomes increasingly common at higher elevations), slightly dented, with short, tapering ears. Occasional red or blue kernels were found in all the fields we sampled and much more rarely a red- or blue-grained plant. Though not highly productive the variety has the ability to mature its ears quickly before the dry season sets in. The plants are characteristically about five or six feet high; they seldom are highly colored, and usually bear one or two ears. They certainly trace back, at least in part, to the "Zapaluta chica" of southern Mexico, a small vigorous white dent which is virtually independent of length of day. It is the basis of much of the early-seasoned white maize of hot and dry areas in Central America and the Caribbean since it has the capacity to hurry on and make an ear before the hot dry weather begins.

To casual inspection the sorghum planted in the valley of the Río Yeguare is exceedingly variable. It is of different heights, and no two plants seem to have the same tassel type, which varies from very open to very dense. Careful study shows that most of the variation is centered in plant height and in the elongation of the tassel branches and that spikelet characters vary little or not at all from plant to plant. Specimens submitted to Snowden, the monographer of the cultivated Sorghums, were identified as *Sorghum caffrorum* var. *glabrescens*, a variety widely distributed in the Old and New World.

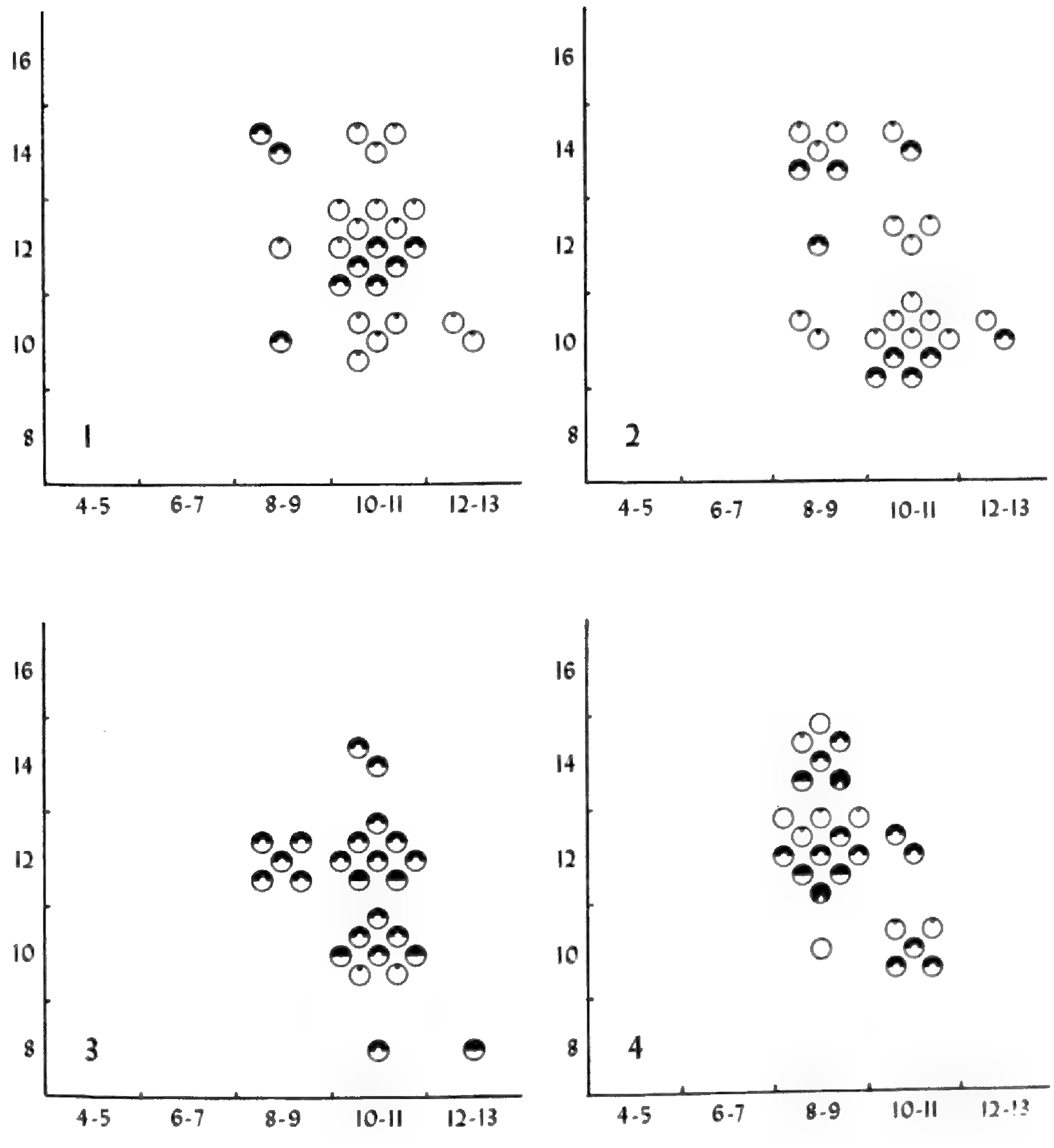
EXPLANATION OF PLATE

PLATE 4

Pictorialized scatter diagrams analyzing the variation in the same four samples of maize as shown in pls. 7 and 8, some of the ears of which are illustrated in those plates. Each sample consists of 25 ears chosen at random from the maize crib. Each circle represents a single ear, and the shape of the circle (see Anderson, Ann. Mo. Bot. Gard. 34:433–467. 1947) indicates that none of these ears bore pointed grains. The position of the circle shows the kernel width in mm. (horizontal scale) and the number of rows of kernels per ear (vertical scale). Open circles represent flinty ears with no apparent soft starch. The greater the degree of black the more soft starch (usually, but not inevitably, accompanied by denting of the kernel). For instance, in diagram 3, the circular glyph at the right represents an 8-rowed ear with kernels 12–13 mm. wide. Its kernels are unpointed and have a heavy deposit of soft starch. Other information from these four collections is as follows:

	No. 1	No. 2	No. 3	No. 4
Average mid-ear width	43 mm.	41 mm.	41 mm.	40 mm.
Average kernel thickness	41 mm.	40 mm.	39 mm.	40 mm.
Average shank diameter	12 mm.	11 mm.	12 mm.	10 mm.
Prevailing pericarp color	○	○	○	○
Prevailing aleurone color	○	○	○	○
Prevailing endosperm color	White	Yellow, white	White	White
Cob color	White	White	White	White
Off-types in sample of 25 ears	6 ears with some kernels with colored aleurone	All ears mixed yellow and white	22 ears with some yellow kernels, 6 ears with some kernels with colored aleurone	21 ears with some yellow kernels
Home of proprietor	Agua Amarillo	Santa Clara	Hda. Lizapa	Pedregal

Note how little variation there is between the averages for the four collections.



ANDERSON & WILLIAMS—MAIZE AND SORGHUM

Explanation of Plate

PLATE 5

Two views of planting operations and one of weeding in the same field. Note bases of burned shrubs; planting sticks thrust forward; and two seed pouches on belt of each man.

1

2

3

ANDERSON & WILLIAMS—MAIZE AND SORGHUM

1

2

3

ANDERSON & WILLIAMS—MAIZE AND SORGHUM

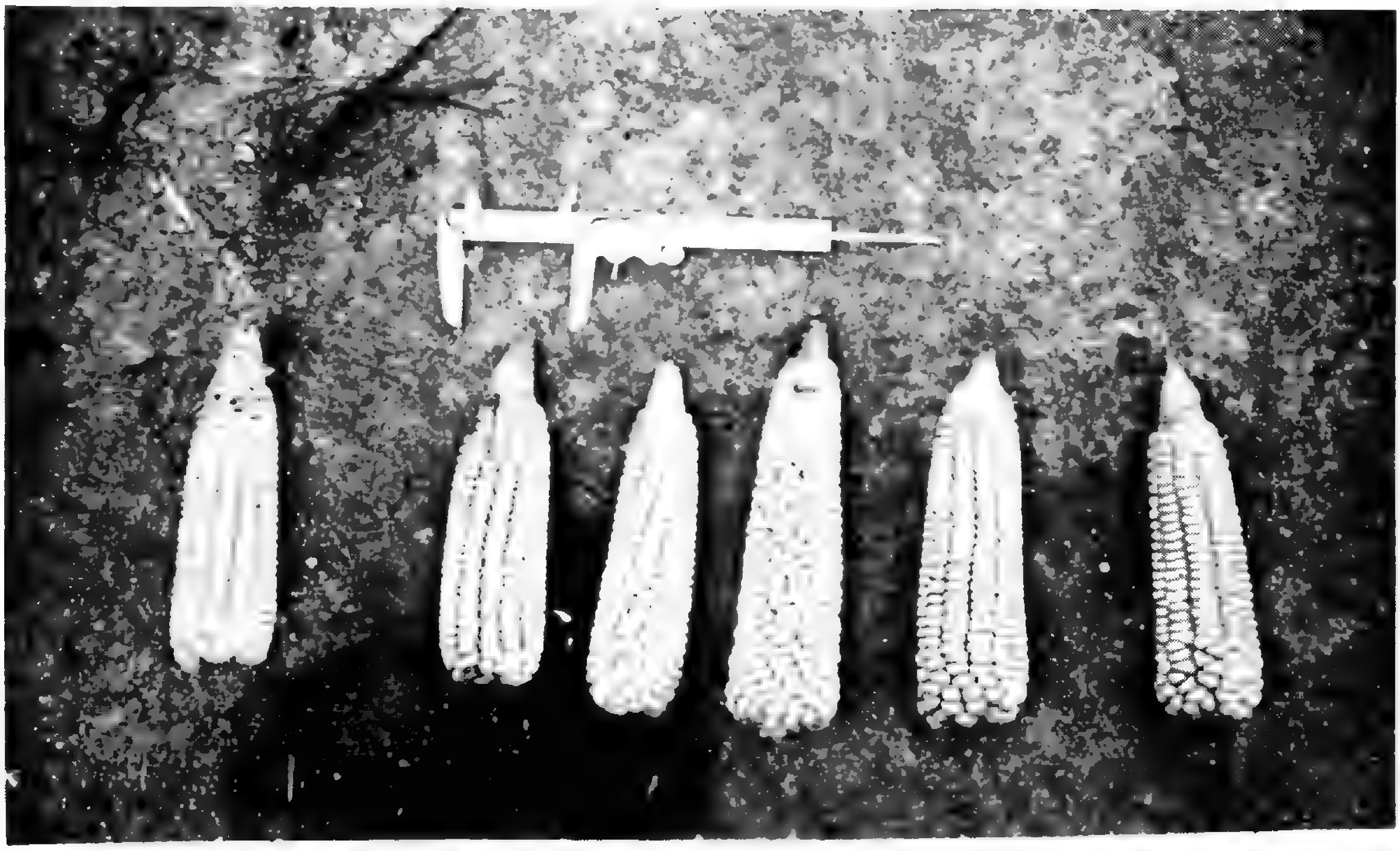
Explanation of Plate

PLATE 6

Fig. 1. The two seed pouches worn by one man, one of leather, the other a *jicara*.

Fig. 2. Paired hills of maize (left) and sorghum (right) just as they begin to show clearly above the soil.

Fig. 3. Maize-sorghum field in late December. The sorghum is not yet quite mature. The maize has been harvested. Its drying tassels can be seen in between the sorghum heads and a little below them. The sorghum in this picture is more uniform in height and panicle than is usual in this area.



1

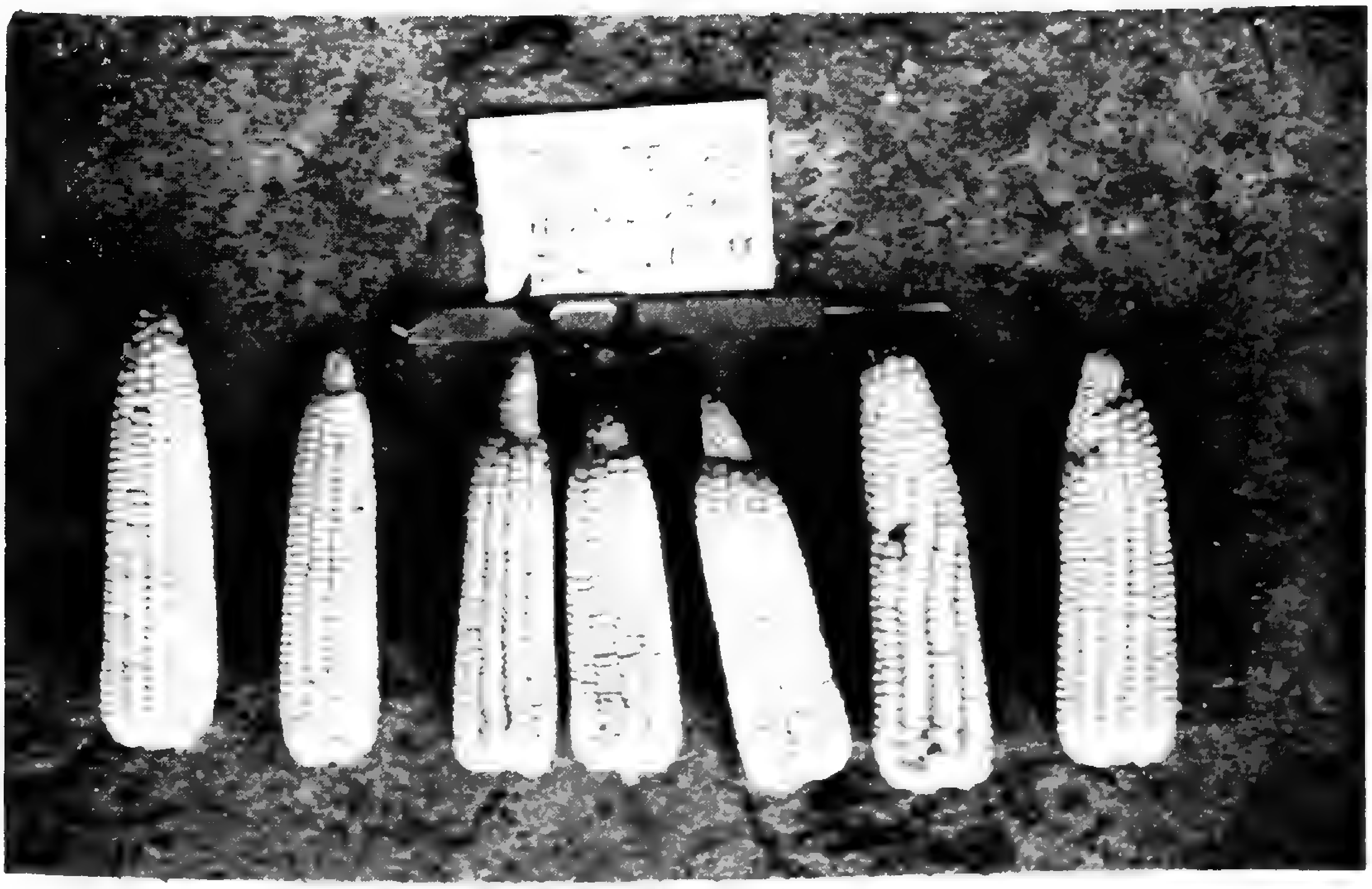
2

Plates 7 and 8. Samples of maize from maize-and-sorghum fields in the valley of the Rio Yeguare. The calipers in each photograph are set at 5 cm. so that the final scale is approximately one-fifth of natural size. Plate 4 shows, under the same numbers (1, 2, 3, 4) used in plates 7 and 8, measurements of samples of 25 ears chosen at random from the maize cribs. Further explanations accompany pl. 4.

Fig. 1. Six ears from the sample studied at Agua Amarillo, Zamorano.

Fig. 2. Two ears and shanks from twelve other ears from Santa Clara, Zamorano.

3



4

Fig. 3. Twenty-four ears from Hacienda Lizapa.

Fig. 4. Seven ears from Pedregal.

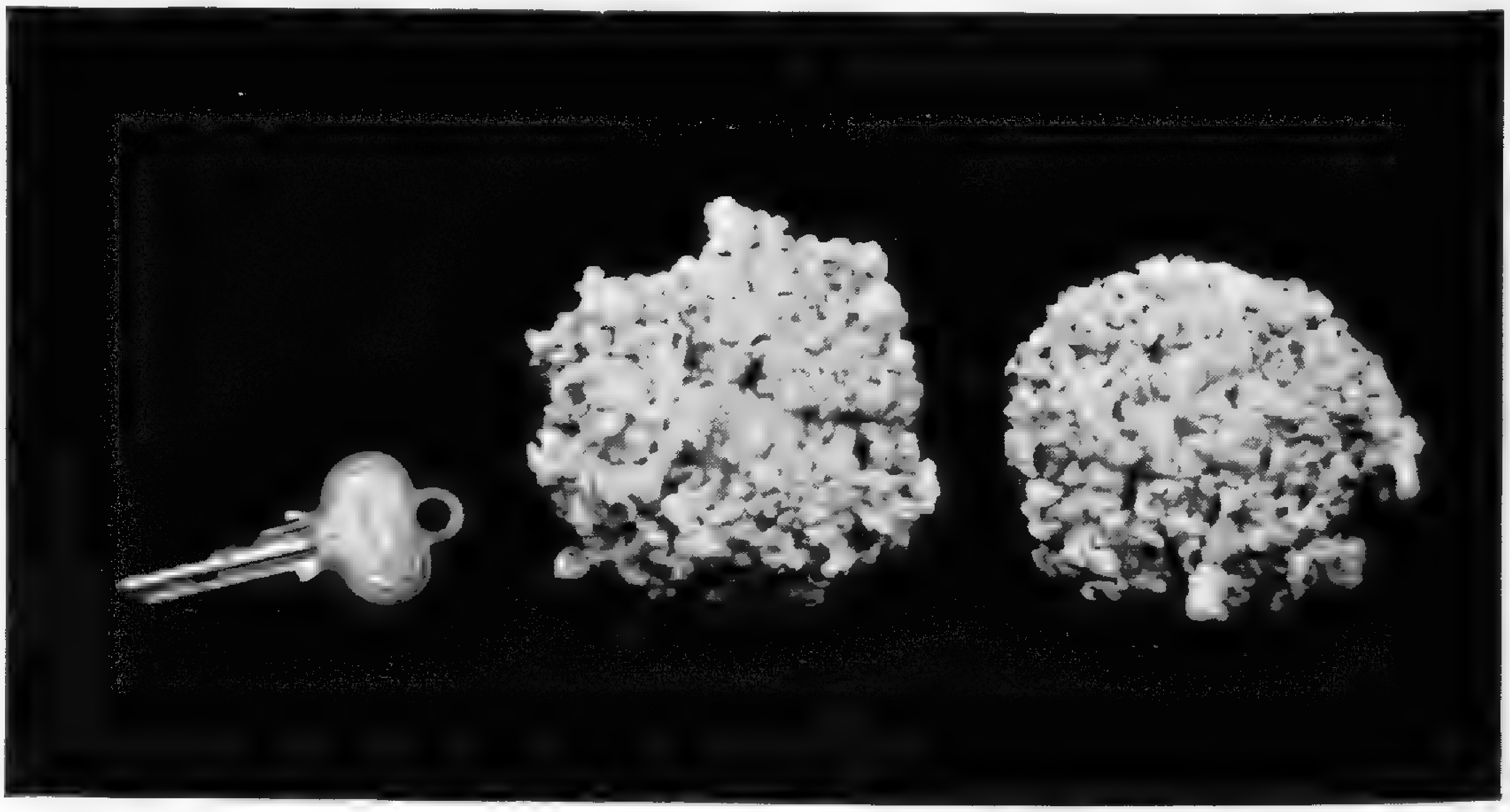
Hacienda Lizapa is on higher land toward the southern end of the valley. The other three collections were from maize grown by families who live just above the valley and operate fields in the valley.

APPENDIX

Notes on Sorghum in Guatemala

JONATHAN SAUER*

A common sight on the streets of Guatemala City and Antigua are the venders of *alborotos*—gaudy red confections like popcorn balls but made of popped sorghum seed. Made in the cities from bought seed, sugar, and artificial coloring, these confections appear no more aboriginal than "Cracker Jack." However, another kind of *alboroto* is occasionally brought into the city markets by the Indians. These are sticky brown cakes, made at home by the farmers from their own sorghum seeds which are popped over a *comal*, spread out in an inch-thick layer on a flat surface, crude brown sugar syrup poured on as a binder, and then cut into little squares.



Alborotos as sold on the streets of Guatemala City

This primitive confection is brought mostly from villages 15 or 20 miles to the north, particularly San Raimundo and San Juan Sacatepequez.[1] In this same area cultivated sorghum was observed at several other villages: San Pedro Ayampuc, Chuarrancho, and San Martin Jilotepeque. Cultivation is general but usually on a very small scale, a few plants being grown near the houses or in cornfields. The sorghum, or *maicillo,* is planted with the start of the rains in May and is harvested after about six months. The prime use is for *alborotos,* but the seed are occasionally cooked and milled into *masa* for *tortillas* and *atole* in all these villages.

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[1] This is the area where *nihuas*, cakes of popped amaranth seed, are prepared; quite often some amaranth seed is mixed with the sorghum in making *alborotos*. The word *alboroto* is translatable as disturbance or tumult; however, if it were derived from a corruption of *alborozo*, it would be translatable as merriment or gaiety, which is also the translation of *alegria*, the general name for popped amaranth cakes in Mexico.

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Outside of this particular group of villages, sorghum cultivation appears to have a wide but spotty distribution in the Republic. It is shipped into Guatemala City commercially from Amatitlán to the south, and from Chiquimula and Jutiapa to the southeast. At Chiquimula and the nearby village of Jocotan, close to the Honduras border, *alborotos* are made and sorghum is ground and mixed with corn meal in times of scarcity. Off in the northwest of the Republic at Sacapulas, sorghum is grown for *alborotos* and occasionally milled. Here, as well as in Baja Verapáz, the roots are said to be perennial, with new shoots coming up every year. Far to the north at La Libertad in the central Petén, Swallen[2] reports *maicillo* (*Sorghum vulgare* Pers.) as commonly cultivated for confections and *atolillos*. Seeds were collected at San Martin Jilotepeque, Depto. Chimaltenango; Amatitlán and San Pedro Ayampuc, Depto. Guatemala; Sacapulas, Depto. El Quiche; and Chiquimula, Depto. Chiquimula. Plant specimens grown from them are deposited in the herbarium of the Missouri Botanical Garden.

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[2] Swallen, J. R. The Grasses of British Honduras and the Petén, Guatemala. Botany of the Maya Area, Misc. Papers 9:187. Carn. Inst. Wash., Publ. 461. 1936.

THE TROPICAL AMERICAN GENUS *TACHIGALIA* AUBL. (CAESALPINIACEAE)*

JOHN D. DWYER**

As in most caesalpiniaceous genera with a center of distribution in the Amazon, one can divide the taxonomic history of *Tachigalia* into two broad periods: the first dominated by the classical works of such authors as Tulasne and Bentham, the second by the brilliant studies of Harms, Ducke, and other recent authors. Of the 22 species of *Tachigalia* recognized in this paper, Ducke has described six. Only one, *T. alba* Ducke, has been reduced to the status of a variety.

Throughout the history of *Tachigalia* most workers have readily linked it to *Sclerolobium,* a strictly tropical American genus with a center of distribution in the Amazon. Paradoxically, Bentham[1] segregated the two genera, placing *Tachigalia* in the Tribe *Amherstieae* and *Sclerolobium* as the type genus of the *Sclerolobieae.* He challenged Tulasne's remark as to the "grande affinité" between the two genera, stating that *Tachigalia* "a quo tamen meo judicio essentialiter differt floribus obliquis et stipite ovarii calycis tubo uno adnato v. saltem supra basin affixo." In my opinion there is no basis for Bentham's segregation. The vast Tribe *Amherstieae,* with more than 65 genera distributed throughout the warmer climates of the world, exhibits an extraordinary meshwork of generic lines. Certainly the central position of the stipe of the ovary is not a character of sufficient strength to warrant the exclusion of *Sclerolobium* from the tribe. In fact, the fruiting material of the two is so similar morphologically that at times it is impossible to tell them apart. Floristically, the principal differences between the two genera lie in the attachment of the stipe of the pistil, in the character of the pubescence of the perianth parts, and in the pattern of the inflorescence. One species, *T. formicarum* Harms, is not readily separated from *Sclerolobium* and may well prove a strong enough link between the two genera to warrant challenging their segregation.

I feel that my work stresses the structure of the flower more than has been attempted in the past. Four floral characters are of great significance in *Tachigalia:* (1) the shape of the receptacle-cup; (2) the shape, and, to some degree, the pubescence of the filaments of the stamens; (3) the pubescence of the petals; and (4) the general character of the stipe of the pistil. In the descriptions of many authors the great variability of the vegetative structures has been disregarded, e.g. the variation in the number of leaflets, the character of the pubescences of the leaves, the number of stipule segments, and the myrmecodomatia of the petioles.

In my formal descriptions of the species of *Tachigalia* I refer constantly to the "lax paniculate inflorescence" and to the "receptacle-cup as seen in hemisection." These terms may require clarification.

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[1] Bentham, George. Caesalpineae. In Mart. Fl. Bras. 15^2:41–254. 1876.

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Actually the term "paniculate inflorescence" is used for convenience, inasmuch as the flowering mass gives the general "impression" of a panicle. On closer examination, however, it is evident that most of the lateral branches arise individually from the axils of the leaves and in reality are racemes. However, in pluriramose inflorescences in which the uppermost leaves are deciduous, the fundamental arrangement of the flowers is so obscured that it is well to adhere to the traditional description of it as a panicle.

I have given considerable emphasis to the morphology of the receptacle-cup and to the stipe of the pistil.[2] In describing the receptacle I refer constantly to a "hemisection" of the cup. A hemisection is best made by taking a scalpel with a broad and thin blade and laying it flat against the upper half of the flat side of the ovary (the sepals, petals, and stamens having been removed under a dissecting microscope); the blade is then pushed through the wall of the cup; the latter may be coriaceous and resistant. Inasmuch as the receptacle-cup varies from being very inequilateral to subequilateral (cf. fig. 1), we may measure a short side and a long side, using the apex of the pedicel as a point of reference. The measurements are made on the part of the cup retaining the stipe of the pistil.

Myrmecophily

The name and much of the fame of *Tachigalia* rest to some degree on the fact that many of the species have the foliage and the inflorescence partly altered by the work of insects (ants, beetles, and coccids). As Bailey[3] points out, "*T. paniculata* Aubl. (type species) was described in 1775 by Aublet, who derived the generic name from "tachigali", a word used by the Indians of the Guianas in referring to trees inhabited by stinging ants, "*tachi*", of the genus *Pseudomyrma*.[4]

While it is not within the province of this paper to take up the fascinating topic of myrmecophily, nevertheless it is necessary to present certain points relating to it. Myrmecophily is not unusual in the families of flowering plants. In the *Caesalpiniaceae* it occurs in only three strictly New World genera: *Tachigalia, Sclerolobium* Vog. and *Platymiscium* Vog. Two species of *Sclerolobium, S. physophorum* Huber and *S. odoratissimum* Spruce ex Benth., are known to be myrmecophilous.[5] The fact that this condition is common in these two genera in the New World suggests a close kinship.

Myrmecophily is by no means universal in the genus *Tachigalia*. In more than 114 collections examined only 36 showed evidence of myrmecodomatia. The most

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[2] At least one contemporary student of the African genera of the Tribe *Amherstieae*, J. Léonard (Bull. Jard. Bot. Brux. 21:376. 1951) is devoting considerable attention to this structure. *Tachigalia* appears to be closely related to his African genus *Lebrunniodendron*.

[3] Bailey, I. W. Notes on neotropical ant-plants. II. *Tachigalia paniculata* Aubl. Bot. Gaz. 75:27–41. 1922.

[4] No doubt the presence of stinging ants on the tachigalia trees accounts for the relative paucity of collections made.

[5] Recently I found several sheets of a collection of Krukoff (*8898*, F, MO, US) which I have identified as *S. odoratissimum*. It is from São Paulo de Olivença, basin of creek, Belém, Amazonas, Brazil. It is apparently the second collection of the species, the type having been collected by Spruce at Rio Negro, Cucuí, Amazonas, Brazil.

striking instance of the absence of myrmecodomatia is in the well-collected species, *T. pubiflora* Benth. The works of Bailey[6] and Bequaert[7] provide us with the bulk of data on myrmecophily in plants, although only one species of *Tachigalia* was studied, *T. paniculata*.

Apparently in the immature leaves the initial swelling at the base of the petiole is not induced by insect action but is a "normal hypertrophy" of the leaf-base. This is the first step in a normal process culminating in the establishment of "hollow petioles and rachises of adult sun plants." This natural hollowing-out process, independent of insect work, results in a petiole which may support the heavy pairs of leaflets of the adult plant. However, the usual fate of the normal hypertrophies of the juvenile petioles of seedlings growing in shade is to be attacked by two species of ants.[8] Whether this attack is responsible for the petiole and the rachis of the inflorescences being so radically altered in such species as *T. formicarum*, *T. rusbyi*, and *T. cavipes* is not known. It would seem logical, however, to consider this condition to be due in part to the work of insects.

From a taxonomic viewpoint Bailey's studies on the single species *T. paniculata* may serve to suggest the possible sequence of steps involved in the maturation of the leaves of all of the tachigalias. In the juvenile plants of *T. paniculata* growing in shade the petioles show a distinct basal enlargement (the potential myrmecodomatium) while in older plants exposed leaves show a more fasciated character (cf. loc. cit., fig. 1). According to Bailey, the young leaves are widely separated under weak light; when the saplings grow in exposed light the leaves change to a yellow or red-brown and "become thick, coriaceous, closely crowded, pendant, and conspicuously embossed-reticulate on the upper surface when dry, and the large foliaceous stipules are palmately multifid."

I have observed that there is a correlation between the pubescence of the leaflets of most tachigalias and the degree of coriaceousness of their texture; i.e. the thicker leaflets tend to be only pubescent to subglabrous while the thinner blades as a rule are densely pubescent. Inasmuch as Bailey's findings on *T. paniculata* indicate the role of environmental factors in the thickness of the leaflets, I feel that the character of the pubescence is difficult to interpret in the absence of mass collections of the species. I have attempted in my study to employ it with moderation as a critical character (cf. my key). It apparently is of especial significance in such species as *T. pubiflora*, *T. myrmecophila*, *T. venusta*, and *T. rigida* where the pubescence of

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[6] Bot. Gaz. 75:27–41. 1922; The anatomy of certain plants from the Belgian Congo, with special reference to myrmecophytism. In Wheeler, W. M. Ants of the Belgian Congo. Amer. Mus. Nat. Hist. Bull. 45:585–621. *pls. 30–45.* 1921–1922.

[7] Bequaert, J. Ants in their relation to the plant world. In Wheeler, W. M. Ants of the Belgian Congo. Amer. Mus. Nat. Hist. Bull. 45:333–583. *pls. 26–29.* 1921–1922.

[8] Bailey (Bot. Gaz. 75:33) states that he and Wheeler "found more than 30 different species of ants in the inflated petioles of juvenile plants. Seven of these are definitely attached to *Tachigalia* as their host plants, and may be designated as 'obligatory', whereas most of the others are facultative, i.e. inquilines which take possession of old domatia that have been abandoned by previous tenants." Both the beetles and ants use "the hollow foliar axes as . . . . nesting chambers . . . . The beetles eat the parenchyma of the medullary rays and obtain liquid carbohydrates from herds of coccids which graze upon it."

the leaflets seems to persist. It must be admitted, however, that all of these species with the exception of *T. pubiflora* are known only from a few collections.

The following statement of Bailey's should serve as a warning to those attempting to identify *Tachigalia* and perhaps many genera of the Caesalpiniaceae: "In fact, the vegetative characters of dominant trees are so unlike those of young suppressed individuals that it is difficult to realize that the two types of plants actually belong to a single species." In my opinion this is substantial reason, in light ot the paucity of material in *Tachigalia*, for using vegetative characters very judiciously. Considering that the fruits of the tachigalias are so poorly known, one can readily understand the importance of floral characters.[9]

Acknowledgments

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Arnold Arboretum, Jamaica Plain, Mass. (A).
Chicago Natural History Museum, Chicago, Ill. (F).
Missouri Botanical Garden, St. Louis, Mo. (MO).
New York Botanical Garden, New York, N. Y. (NY).
Jardin des Plantes, Muséum National d'Histoire Naturelle, Paris (P).
U. S. National Herbarium, Washington, D. C. (US).

Taxonomy

TACHIGALIA Aubl. Hist. Pl. Guin. 1:372. 1775.

Cuba Scop. Introd. 300. 1777.
Valentina Neck. Elem. 2:450. 1790.
Tachia Pers. Syn. Pl. 1:459. 1805.
Tassia Rich. ex D.C. Prodr. 2:487. 1825.

Small or large trees; stipules paired, segmented, the laminae foliose; leaflets 3- to 15-jugate, pairs opposite (occasionally alternate in *T. multijuga*), the upper pairs usually larger than the basal pair; leaflets chartaceous to coriaceous, usually inequilateral, the costa prominent beneath, the secondary veins (1–) 2–20 per side, arcuate-ascending, acuminate at apex, obtuse, cuneate, auriculate or cordate at base, the margin slender-callose, often subrevolute, rarely bullate (?); petioles often myrmecophilous at base or rarely along entire length, angular (often subtriangular) to biconvex in cross-section, nodose at petiolule attachment; petiolules short; in-

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[9] It is remarkable that very few collections bear legumes of any appreciable size; in fact the fruits of only 6 of the 22 species have been described. In my opinion, the mature fruit of the tachigalias is probably dehiscent, despite several descriptions to the contrary. One collection of *T. venusta, Capucho 418* (F), has an excellent dehiscent fruit.

florescence "lax-paniculate," the central rachis occasionally myrmecophilous, the flowers disposed in dense racemes; bracteoles of mature flowers soon deciduous, subulate, pubescent; receptacle-cup campanulate, urceolate, cylindrical, or subtriangular, the sides as seen in hemisection subequal to obviously unequal, pubescent on outside, glabrous and often furfurcaceous (ant eggs?) within; sepals 5, imbricate, reflexed at anthesis, pubescent, the 2 outermost smaller and thicker, the margin ciliolate to ciliate; petals 5, yellow to white, rarely orange in vivo, subequal, petaloid to carnose, often subclawed at base; stamens 10 (rarely 15–16), unequal in length, the filaments uniform, or 7 obviously longer, more slender and subulate, the other 3 often conspicuously reduced, more falcate or sigmoidal, and thicker in middle, the entire complement of filaments pubescent at base on inside (in one species one filament glabrous in toto), often pubescent at base on outside, the anthers glabrous, versatile, dehiscing longitudinally; stipe of pistil never with strict central attachment, the ovary narrow-oblong, densely pubescent throughout, the ovules 4–15, the style elongate, scattered pubescent below, the stigma capitate, rarely bifid; fruit short-stipitate, oblong, flat, thin, the coriaceous valves apparently completely separating at maturity, the seed solitary, surrounded by a subligneous and thin wing as broad as the valves.

Nomenclatural type: *Tachigalia paniculata* Aubl.

KEY TO THE SPECIES

a. Filaments of all stamens pubescent at base; pubescence of ovary uniformly distributed; South America.
b. Principal secondary veins of leaflets 5–20.
c. Stamens 10 (–11).
d. Leaflets essentially glabrous; receptacle-cup elongate-turbinate or cylindrical, tapering on wider side, about 10± mm. long, the hairs dense, subappressed; staminal filaments 1.5–2.2 mm. wide.
e. Leaflets 4- to 8-jugate, the costa prominent on upper side........................1. *T. longiflora*
ee. Leaflets 3-jugate, the costa almost plane on upper side................................2. *T. catingae*
dd. Leaflets pubescent (often microscopically); receptacle-cup irregularly urceolate, campanulate, or caliciform, up to 8 mm. long; petals white to yellow in vivo, densely to sparsely pubescent within, rarely ferrugineous; staminal filaments up to 1.5 mm. wide.
e. Leaflets 8- to 13-jugate ....3. *T. multijuga*
ee. Leaflets 2- to 7-jugate.
f. Leaflets with secondary veins immersed above, margins obviously revolute; inflorescence completely ferrugineous to velutinous; margins of sepals densely ciliate ....4. *T. rigida*
ff. Leaflets with secondary veins plane to prominulous above, margins scarcely revolute; inflorescence at most moderately velutinous; margins of sepals ciliolate.
g. Leaflets glabrous above (except the costa), subequilateral; bracteoles equal to or exceeding the mature buds...5. *T. bracteolata*
gg. Leaflets sericeous, often velutinous beneath, obviously inequilateral; bracteoles not exceeding the mature buds, usually fugacious.
h. Longer side of receptacle-cup as seen in hemisection (4–)5–9 mm. long.
i. Wall of receptacle-cup 0.2–0.9(–1) mm. thick.
j. Leaflets (2–)4- to 7-jugate, the costa prominulous to plane above.
k. Mature leaflets densely sericeous below and (usually) above.
l. Leaflets tapering subacutely at base; rachis of inflorescence swollen (3.5–5 mm. wide at base) ....6. *T. cavipes* ✓
ll. Leaflets tapering sharply, or very obtuse to subauriculate at base; rachis of inflorescence 1–3 mm. wide at base.

m. Petioles with myrmecodomatia; juvenile and mature leaflets sericeous and velutinous on both sides, the principal secondary veins usually 6, arcuate; stipe of ovary basal and suberect in a short urceolate cup with subequal sides; fruit up to 15 cm. long; Brazil........7. *T. venusta*

mm. Petioles without myrmecodomatia; juvenile leaflets sericeous beneath, the older ones often sparsely puberulent beneath, the principal secondary veins 8–12; stipe of ovary curving arcuately, arising 1.5–2 mm. above base of an obviously inequilateral cup; fruit up to 11 cm. long; British Guiana........8. *T. pubiflora*

kk. Mature leaflets merely puberulent beneath........9. *T. paniculata*

jj. Leaflets 2- to 4-jugate, the costa prominent above........10. *T. ulei*

ii. Wall of receptacle-cup 0.8–1.4 mm. thick; basal hairs of thicker staminal filaments scattered........11. *T. plumbea*

hh. Longer side of receptacle-cup as seen in hemisection 1–4(–5) mm. long.

i. Stipules about 6 cm. long........12. *T. grandistipulata*

ii. Stipules 1.5–4 cm. long.

j. Leaflets 2- to 4-jugate, densely sericeo-puberulent at maturity........13. *T. myrmecophila*

jj. Leaflets 4- to 12-jugate, moderately puberulent to subglabrous.

k. Petioles and branches swollen; sides of receptacle-cup as seen in hemisection almost equal; petals not exceeding largest sepals in length, the long hairs extending beyond margins........14. *T. formicarum*

kk. Petioles and branches not greatly swollen; sides of receptacle-cup as seen in hemisection obviously unequal; petals exceeding largest sepals in length, with hairs not projecting beyond margins.

l. Leaflets 7- to 12-jugate; receptacle-cup inequilaterally subrotund........15. *T. polyphylla*

ll. Leaflets 6- to 10- (rarely 12-) jugate; receptacle-cup inequilaterally caliciform.

m. Leaflets chartaceous........16. *T. agyrophylla*

mm. Leaflets coriaceous.

n. Filaments of stamens dimorphic, 5–10 mm. long; stipe of pistil 2(–3)–7 mm. long.

o. Bracteoles narrow at base, 4–6 mm. long; stipe of pistil up to 3 mm. long........17. *T. rusbyi*

oo. Bracteoles swollen at base, up to 2 mm. long; stipe of pistil (3–)4–8 mm. long........18. *T. pulchra*

nn. Filaments of stamens submonomorphic, 5–6.5 mm. long; stipe of pistil up to 1.5 mm. long........19. *T. tessmannii*

cc. Stamens 15 (–19)........20. *T. macrostachya*

bb. Principal secondary veins of leaflets 1–3........21. *T. ptychophysca*

aa. Filaments of stamens pubescent at base, except one filament entirely glabrous; hairs of ovary disposed in longitudinal rows; Costa Rica........22. *T. versicolor*

1. **TACHIGALIA LONGIFLORA** Ducke, in Arch. Inst. Biol. Veg. 2:38–39. 1935. (*T.: Ducke 24291!*).

Small trees; ultimate twigs smooth, waxy on surface, drying purple-black, glabrous; stipules not seen; leaves up to 0.5 m. long; petioles triangular in cross-section below, about 0.5 cm. wide, up to 40 cm. long, plano-convex toward apex (about 0.4 mm. wide), drying purple-black; petiolules smooth, glabrous, tumescent, somewhat flattened on one side, up to 5 mm. long, more than half as broad; leaflets 4- to 8-jugate, stiff, coriaceous, glabrous, subequilateral, obovate-oblong or lanceolate, up to 18 cm. long, up to 6.5 cm. wide, acuminate at apex, acute, obtuse and distinctly inequilateral at base, the costa prominent above and below, almost plane beneath proximally, about 2 mm. wide at base, the principal secondary veins 7–8, arcuate-ascending, those in middle of blade 2–3 cm. apart, prominent, the reticulations lax, prominulous, the margin scarcely revolute; inflorescence lax-paniculate, the branches few, shorter than the leaves, densely tomentose, widely arcuate-ascending; bracteoles densely tomentose, cuneate-subulate, about 5 mm. long, very acute, subplane below tip; buds falcate-oblong, up to 1.6 cm. long, the pedicels about 2 mm. long; receptacle-cup long-turbinate, very coriaceous, the wall about 1 mm. thick, pubescent on outside, the two sides as seen in hemisection about 9 mm. long; sepals 5, carnose-subcoriaceous, finely velutinous on both sides, ovate-oblong to oblong-subrotund, 8–11 mm. long, 6–8 mm. wide, obtuse at apex, the margin ciliolate with minute black glandular bodies amid the ciliolations, the latter often interspersed with more appressed coarse hairs within; petals orange-yellow in vivo, carnose-subcoriaceous, subpellucid, long appressed-hirsute within, concave, linear-oblong to oblong, 10–12 mm. long, 5–7 mm. wide, obviously obtuse at apex, distinctly clawed for 3 mm. at base (or the largest non-clawed and subcordate at base); stamens 10, the filaments of 7 linear-subulate, 18–22 mm. long, bearded only at base within, the other 3 thick-falcate, as wide as or wider at middle as/than at base (1.7–2.2 mm. wide in middle), entirely glabrous or with a few scattered hairs at the base; stipe of ovary slender, pubescent, about 4 mm. long, arising less than a mm. above very base of receptacle-cup, suberect, the ovary linear-rectangular, up to 8 mm. long, the style elongate, up to 14 mm. long; fruit unknown.

Brazil: amazonas: São Paulo de Olivença, Rio Solimoes, *Ducke 24291* (F, P).

T. longiflora, known from this solitary collection, is a sharply defined species; it is readily linked with *T. catingae* Ducke. The foliage of both species is essentially glabrous. Both possess a receptacle-cup turbinate in shape and tapering gradually on the wider side. The long dense ferrugineous hairs on the inner surface of the petals are strikingly different from those of any other species. The orange petals of the living flowers readily segregate *T. longiflora* and *T. catingae* from other species of *Tachigalia.*[10]

2. Tachigalia catingae Ducke, in Arch. Inst. Biol. Veg. 4:12–13. 1938. (T.: *Ducke 35421*!).

Low tree; terminal twigs rotund in cross-section, smooth, minutely pubescent; stipules foliose, with two large plane subequal segments, ovate-triangular, up to 2.2 cm. long, acute, the inner one often with a shorter subulate segment at base; leaves up to 30 cm. long; petiole angular in cross-section, obviously canaliculate, glabrous, about 3 mm. wide at base, myrmecodomatium tumescent, about 2 cm. above point of articulation, elliptic-oblong, about 4 cm. long, about 0.8 cm. wide; petiolules subtumescent, glabrous, about 8 mm. long, 4 mm. wide; leaflets of 3 opposite pairs, coriaceous, drying dull tan above and below, glabrous throughout, subequilateral, wide-oblong, about twice as long as broad, up to 20 cm. long, up to 10 cm. wide, long-acuminate (acumen up to 2 cm. long), ultimately obtuse at

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[10] One collection of *T. pubiflora* made by Abraham in British Guiana states on the label that the flowers are orange to cream-colored.

apex, obtuse and obviously inequilateral at base, the costa subplane, glabrous above, subprominent to prominent and glabrous beneath, up to 2.5 mm. wide at base in largest leaflets, the principal secondary veins 6 ±, distinctly arcuate-ascending, prominulous to scarcely evident above, more evident beneath, the reticulations ultimately very small and as evident as secondary veins above, conspicuous beneath, the margin thin-callose, somewhat revolute; inflorescence widely lax-paniculate, rotund in outline, the central rachis ferrugineous, subangular and articulate toward apex, up to 14 cm. long, the branches gracefully and widely arcuate-ascending, about same length as central rachis; bracteoles small, subulate, concave, pubescent, up to 3 mm. long; flowers subsessile, the buds inequilaterally obovate, about 8 mm. long; sepals 5, ferrugineous-puberulent, 2 of these thicker, concave, oblong to oblong-rotund, 6 mm. long, the others 7.5–1 cm. long, 0.8 cm. wide, obtuse, the margin ciliolate with minute glandular excrescences interspersed; petals orange-yellow in vivo, thin-carnose, concave, appressed-sericeous within, pubescent on outside, with small glandular bodies about 0.2 cm. long on inner side at base, oblong to oblong-rotund, up to 1 cm. long, 6 mm. wide, ciliolate on margin; stamens 10, 7 filaments subulate above middle, up to 14 mm. long, about 0.7–0.9 mm. wide at base, 0.5 mm. wide at middle, densely hirsute at base on inside, the remaining 3 filaments scarcely tapering except at very tip, about 1.5 mm. wide at base, the anthers of 7 filaments about 2 mm. long, those of 3 filaments about 1.2 mm. long; receptacle-cup inequilaterally cylindrical, tapering only gradually at base, the wall coriaceous, about 0.7 mm. thick as seen in hemisection, the longer side about 10 mm. long and shorter side about 7.5 mm. long; stipe of pistil elongate, upright, pubescent, attached about 1 mm. above center of receptacle-cup, about 5 mm. long, about 0.7 mm. wide, the ovary ferrugineous-sericeous, elongate-rectangular, about 7 mm. long, about 0.2 mm. wide, the style about 1 cm. long, scattered-villose for about two-thirds its length.

Brazil: amazonas: Upper Rio Curicuriary, Rio Negro, *Ducke 35421* (P, US).

This species is readily recognized by its very large leaves (the widest observed in any species of the genus), with leaflets few-jugate and essentially glabrous. According to Ducke, it is a common tree of the well-known *catingas* of the Rio Negro.

3. Tachigalia multijuga Benth. in Mart. Fl. Bras. 15^2:230. 1876.

Large tree; terminal twigs smooth, round in cross-section, densely puberulent, longitudinally canaliculate; leaves up to 40 cm. long; stipules not seen; petioles up to 25 cm. long, subrotund to angular or squarrose in cross-section, ultimately virgate, 0.2–0.25 cm. wide at base, villose with erect but apically flexed hairs; petiolules almost smooth, pubescent, squarrose in cross-section, up to 5 mm. long, 1–1.5 mm. wide; leaflets 8- to 13-jugate, thin-coriaceous, pubescent to glabrous above, pubescent to subglabrous below, usually drying chocolate-brown beneath, oblong to narrow-oblong, up to 11 cm. long, up to 3.2 cm. wide, those at middle of leaf often larger than terminal or subterminal ones, distinctly acuminate (the acumination ultimately acute), inequilateral and obtuse at base, the costa subimmersed above, prominent beneath, often pubescent only at base, about 0.3–0.4 mm. at middle of lamina, the principal secondary veins 6–10, prominulous above, prominulous to prominent beneath; inflorescence lax-paniculate, the central rachis up to 25 cm. long, about 0.35 cm. wide at base, densely pubescent, the branches lax-arcuate or often sharply divergent, up to 18 cm. long, the racemes narrow-pyramidal; bracteoles densely pubescent (often ferrugineous), subulate, up to about 11 mm. long, acute; buds narrowly obovate or widely obpyriform, up to 1.5 cm. long; receptacle-cup cylindrical or cup-shaped, often ferrugineous on outside, the wall carnose, 0.4–0.8 mm. thick, the longer side as seen in hemisection (5–) 7–10 mm. long, the shorter side (4–)5–7 mm. long; sepals 5, 2 smaller, all stiff-carnose or subcoriaceous, velutinous or ferrugineous-pubescent on inside and outside, oblong, ovate-oblong to subrotund, 4.5–9(–12) mm. long, 3.5–7 mm. wide, acute or obtuse at apex, the margin densely ciliolate; petals yellow in vivo, appressed-hirsute within, usually glabrous on outside (occasional flaring hairs at base), oblong to obovate-oblong, 6.5–7 mm. long, 4.5–5 mm. wide, obtuse at apex, somewhat clawed to obviously clawed at base; stamens 10, the filaments of 3 shorter or more widely subulate (0.6–1.2 mm. wide in middle), all 7–10 mm. long, about 1 mm. wide at very base, the hairs restricted to lowest quadrant on inside, the 7 remaining filaments more narrow-subulate, up to 1.4 mm. wide in middle, the anthers about 2.2 mm. long; stipe of pistil attached about 1 mm. above center of base of cup, suberect, 6 ± mm. long, the ovary velutinous, oblong, 4–6 mm. long, 2–2.5 mm. wide in middle, the style 12 ± mm. long; fruit (here apparently immature), coriaceous, oblong, up to 9 cm. long, 3 cm. wide, very obtuse at apex, subcuneate at base.

BRAZIL: Without locality, *Lund s. n.* (P); *Glaziou 2996* (P); AMAZONAS: Capoeiras near Uananuca, Rio Negro, *Spruce 2022* (P); SÃO PAULO: Santos, *Mosén 3370* (P); RIO DE JANEIRO: Serra dos Orgaos, *Glaziou 11909* (P); banks of Tijuca, *Riedel & Luschnatt 1253* (A, NY); Tijuca, *Riedel & Luschnatt s. n.* (NY).

Only two species of *Tachigalia* have numerous leaflets: *T. multijuga* and *T. polyphylla.* These are readily distinguished, the former having very large buds and flowers, the latter having much smaller ones.

One of the two sheets labelled *Spruce 2022* in the Paris Herbarium shows a specimen in bud and with obviously immature leaflets. The buds are densely ferrugineous-pubescent and are subtended by persistent (?) subulate, ferrugineous stipules. The leaflets are slightly puberulent above and densely so beneath. I consider this to be *T. multijuga* despite the fact that it does not match, at least with respect to the maturity of its parts, Bentham's original description.

The second sheet, bearing no indication of locality, has foliage fragments of 2 species; one of the leaves is obviously *T. ptychophysca;* the other leaf is, in my opinion, obviously not *Tachigalia.*

There is a beautiful plate (pl. 59) of *T. multijuga* in 'Flora Brasiliensis' (loc. cit.).

4. Tachigalia rigida Ducke, in Arch. Inst. Biol. Veg. Rio de Janeiro 4:12. 1938. (T.: *Ducke 35423!*).

Small trees; ultimate twiglets canaliculate, finely velutinous; stipules not seen; leaves up to 25 cm. long; petioles slender, velutinous, scarcely nodose at petiolule-articulation, with inconspicuous myrmecodomatia 2–2.5 cm. from base, 2.5–3.5 cm. long, 0.5–0.7 cm. wide; petiolules of largest leaflets up to 7 mm. long, about 3 mm. wide, densely velutinous; leaflets 4- to 6-jugate (the lower pairs smaller, 1.5–2.5 cm. apart), subequilateral, subcoriaceous, stiff, drying dull gray-green above, tan beneath when immature, densely velutinous above and below, the hairs often cinnamomeous below, the older leaflets subglabrous above (except costa), narrow-lanceolate to narrowly subovate-lanceolate, up to 12.5 cm. long, up to 3.3 cm. wide, distinctly acuminate (the acumen up to 1 cm. long) at apex, ultimately acute, subcuneate to cuneate-obtuse at base, the costa immersed above and densely tufted-pubescent, very obviously prominent beneath and densely pubescent, about 2 mm. wide proximally, the principal secondary veins 8 to 10, arcuate-ascending, immersed above, prominent beneath, the tertiary veins conspicuous above and below, the ultimate reticulations evanescent, the margin revolute; inflorescence lax-paniculate, the central rachis up to 30 cm. long, up to 0.4 cm. wide at base, velutinous, the pedicel-scars whorled, conspicuous below, the lateral branches few, often exceeding the main axis, the terminal racemes 8–11 cm. long; bracteoles concave, densely pubescent, upright, subulate, swollen at base, up to 6 mm. long; buds at maturity obliquely obovate-rotund; receptacle-cup (including pedicel) caliciform, the wall coriaceous, about 0.8 mm. thick, pubescent on outside, glabrous within, the longer side as seen in hemisection about 9 mm. long, the shorter side about 4 mm. long; sepals 5, 2 obviously smaller, all thin-coriaceous, densely pubescent, the hairs dense, scraggly but subappressed and ferrugineous, oblong, obovate-oblong to subrotund, 8–9 mm. long, 6–7 mm. wide, obtuse at apex and base, the margin densely ciliate; petals 5, yellow in vivo, subequal, thin-carnose, subpellucid, pubescent within and at very base on outside, the subappressed hairs restricted medianly, oblong to oblong-rotund, 8–10 mm. long, 7–8 mm. wide, obtuse at apex, obviously clawed; stamens 10, of which 7 filaments are linear-subulate, up to 20 mm. long, about 0.5 mm. wide in middle, pubescent on both sides at base, the remaining 3 filaments thickly subulate, falcate above, about 8–9 mm. long (without stretching), about 1.1 mm. wide in middle, the hairs dense and irregular below middle, the anthers of the 3 thick filaments about 1.1 mm. long; stipe of pistil often arising just below middle of longer side of cup as seen in hemisection, 3.5–4 mm. long, curving arcuately, the ovary narrow-oblong, about 5 mm. long, 2–2.5 mm. wide, entirely pubescent, the style elongate, the ovules 9–12; fruit not seen.

Venezuela: amazonas: Solano, Lower Casiquiare, *Llewelyn Williams 14810* (F, US). Brazil: amazonas: Rio Negro, Cucuhy, Igarapé Macacuny, *Ducke 35423* (P, US). Colombia: Río Negro, Ríos Guainia & Casiquiare, Cano Ducuruapo (Igarapé Rana), *Schultes & Lopez 9389* (US).

T. rigida is readily recognized by its subequilateral and elliptic leaflets which, when young, have a dense cinnamomeous pubescence on the underside; the pubescence is retained by the mature branches of the inflorescence. The leaflets of both Williams' and Ducke's collections have the secondary veins immersed. This is not encountered in any other species of the genus.

Williams' collection, cited above, makes it clear that the character of the pubescence is variable with the age of the leaflets (cf. remarks in introduction to this paper); the more mature leaflets are subglabrous above. I noted in dissecting the flowers that the stipe of the pistil is attached closer to the base than it is in the other two collections cited. Williams' field notes on his collection *14810* are interesting.[11] The locality indicated on the typewritten label does not agree with the one on the printed label of the herbarium sheet. I have not seen Ducke's *T. rigida* var. *argentea* based on his own collection *35422* from Río Curicuriary, Amazonas, Brazil. He remarks: "A typo differt foliolis junioribus utrinque tomento breviore sericeo subargenteo (nec nervis rufopilosis), foliolis vetustis (supra glabratis), subtus unicoloribus subaureis . . . ." I suspect that the variety will show considerable variation in the pubescence of leaflets of different ages, thus jeopardizing its validity.

5. Tachigalia **bracteolata** Dwyer, sp. nov. (T.: *Martin s. n.!*).

Arbores ?; ramuli terminales minute lenticellati puberuli transverse rotundati tenuiter canaliculati; stipulae simplices lineari-spathulatae proxime lineares apice spathulatae, circ. 10 mm. longae, curvatae (certe deciduae maiores); folia ad 30 cm. longa; petioli puberuli virgati, ad 16 cm. longi, in medio 1–1.2 mm. lati, vix nodosi; petioluli graciles puberuli, ad 5 mm. longi; foliola 3- vel 4-jugata, tenui-coriacea, subglabra (praeter costam), vix inaequilateraliter elliptica vel oblonga (rare ovata), ad 14.5 cm. longa, ad 5.2 cm. lata, apice conspicue acuminata gradatim attenuata basi obtusa, costa tenue (ad 0.8 mm. basi lata) puberula supra prominula infra subprominente, venis secundariis principalibus 4–7 arcuato-ascendentibus supra prominulis infra conspicuis essentialiter glabris, reticulatis venis minimis ultime vix distinctis, marginibus tenui-callosis; inflorescentiae paniculatae foliis breviores, rhachide centrale angulare puberulo, ad 8 cm. longo, circ. 2 mm. basi lato, ramulis virgatis puberulis, racemis dense floriferis, ad 6 cm. longis, bracteolis elongatis non mox deciduis, subulatis, ad 11 mm. longis, saepe maturas gemmas multo excedentibus, marginibus plerumque revolutis; calyx receptaculi inaequilateraliter cylindricus plerumque extus costatus, pariete carnoso, 0.5–0.7 mm. lato, latere longiore 6–8 mm. longo, latere breviore 4–5 mm. longo; sepala 5, ex-

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[11] "Canáchi (Baniba). Arbol de tamano mediano can la corona sebre saliente hacia el río ye de forma irregular; tronco 30 cm. 6 mas de diam., redondo sin ramas por la mitad de la altura; la corteza aspera gris y el loer castaño claro; las flores amarillas en espigasen espigas terminales erectas; la albura de color claro, y el duramen algo mas obscuro no muy bien definido; en la margen arboreada, periodicamente anegada; arriba de Maroa, Río Guainia, alt. 127 m."

teriora 2 crassioria, omnia carnosa vel subcoriacea extus intusque sericea, concavo-oblonga vel oblongo-rotunda, 3.5–7 mm. longa, 3.5–5 mm. lata, marginibus dense ciliolatis; petala carnosa extus glabra intus pubescentia, ciliis longis irregularibus in medio corpore dispositis, oblonga-elliptica vel obovata, 6.5–9 mm. longa, 3.2–4.5 mm. lata, obtusa plerumque basi unguiculata; stamina 10, filamentis 7 lineari-subulatis, ad 15 (?) mm. longis, circ. 0.4–0.6 mm. latis, in medio multos comos basi ferentibus, filamentis 3 reliquis crassioribus falcatis vel suberectis 5–8 mm. longis, circ. 1 mm. in medio latis; stipes ovarii elongatus, 3–4 mm. longus, ad apicem rectus, ovario oblongo, stylo elongato; fructus non visus.

FRENCH GUIANA: Cayenne, *Martin s. n.* (F).

The new species is marked by thin subchartaceous and subequilateral leaflets, virgate petioles, and elongate and persistent (even following anthesis) bracteoles. It is from the character of the latter that the species derives its name. The bracteoles are remarkably revolute. *T. bracteolata* seems to be closely related to *T. paniculata* Aubl.

6. TACHIGALIA CAVIPES (Spruce ex Benth.) Macbr. in Field Mus. Publ. Bot. 13^3:127. 1943.

Tachigalia paniculata Aubl. var. *cavipes* Spruce, ex Benth. in Mart. Fl. Bras. 13^2:229. 1876.

Large tree; twiglets usually round in cross-section, puberulent; stipules divided into 2–3 plane, linear-elliptic, subequal segments arising palmately from a short stalk, the longest up to 1.5 cm. long, about 0.2 mm. wide, attenuate-acuminate; leaves up to 35 cm. long, petioles squarrose to angular in cross-section, often nodose at petiolule articulation, the internodal areas thinner (as narrow as 2 mm., the petiole thus subvirgate), or the entire petiole myrmecophilous, up to 22 cm. long, up to 4 mm. wide, or often with distinct myrmecodomatia at base which are elliptic-falcate in profile, up to 5 cm. long, 0.6–1 cm. wide; petiolules subconvex, slender to tumescent, 0.3–1.3 cm. long; leaflets 3- to 5-jugate, coriaceous, densely puberulent to subglabrous above and below, elliptic-lanceolate or narrow to wide-oblong, the lowermost pairs 5–12 cm. long, 2–5 cm. wide, the upper 15–23 (+?) cm. long, up to 8 cm. wide, definitely acuminate at apex, tapering gradually or even sharply at base, obviously inequilateral at base, the costa plane to plano-convex above, prominent beneath, the secondary veins of larger leaflets 8–12, obviously arcuate-ascending, prominulous above and below, rarely evanescent, the reticulate areas prominulous to subevanescent, the margin subrevolute, vaguely callose; inflorescence terminal, paniculate, the branches few or absent, the central rachis obviously thick, 3–5 mm. wide at base, the pedicel-scars very conspicuous when flowers deciduous, the flowers often very quickly deciduous, the inflorescence becoming few-flowered at tip of rachis, or the racemes very obvious, wedge-shaped or narrow-pyramidal, up to 12 cm. long, up to 3.8 cm. wide at base; bracteoles short, subulate, acute, puberulent; receptacle-cup inequilaterally campanulate, the wall thin-coriaceous, up to 0.8 mm. thick, minutely puberulent on outside, the longer side as seen in hemisection 9–10 mm. long, the shorter side 4.5–8 mm. long, the sepals coriaceous or carnose-coriaceous, concave, pubescent on both sides, oblong to oblong-rotund, 7–8 mm. long, 4–7 mm. wide, obtuse at apex and base, the margin densely ciliolate often with minute glandular bodies interspersed; petals petaloid to thin-subcoriaceous in texture, often vaguely carinate at base, oblong to obpyriform or obovate-rotund, 7.5–10 mm. long, 5.5–7 mm. wide, hirsute within, the hairs concentrated centrally or almost extending to margins, obtuse at apex, distinctly clawed at base; filaments of stamens 10, dimorphic, 7 being slender, subulate, 15–20 mm. long, about 0.3 mm. wide at middle, the other 3 thicker, falcate, up to 11 mm. long, about 0.9 mm. wide at middle, all pubescent at base; stipe of ovary arising about 2 mm. above base of cup, often geniculate in middle, almost equal to shorter side of cup in length, the ovary fusiform to oblong, 4–7.5 mm. long, the style up to 15 (?) mm. long, the ovules 8–9; fruit not seen.

BRAZIL: AMAZONAS: Porto Velho (Rio Madeira), *Ducke 228* (F, NY, MO, US), *35419* (P); Panuré, Rio Vaupes, *Spruce 2553* (MO, photo, NY, P, type collections of *T. paniculata* var. *cavipes*); Rio Negro, San Felippe, *Luetzelburg 22998* (NY); Humayta near Livramento on Rio Livramento, *Krukoff 6816* (MO, US); PARÁ: Belém Utinga, *Ducke 1707* (F, NY, US).

COLOMBIA: VAUPES: Bacuraba Cachoeira, Río Vaupes, e. of Mitú, *Allen 3389* (MO).

PERU: LORETO: Palta-cocha, Upper Río Nanay, *Llewelyn Williams 3192* (F, US).

T. capives has long been related to *T. paniculata* Aubl., as a variety of the species. However, it is readily distinguished from typical *T. paniculata* by its thick floral axis rugose with pedicel scars and bearing larger cuneate-pyramidal racemes. Its receptacle-cup is more campanulate than that of the Aublet species.

Allen 3389, with leaflets superficially like those of *T. pubiflora* Benth., has the floral axis more slender (0.3 mm. wide) than in the other cited collections of *T. cavipes*. However, it has the characteristic pedicel scars of the latter species. It is well to note that this specimen has an obvious myrmecodomatium at the base of the petiole which is smaller than in its Brazilian counterparts. Perhaps there is a correlation between the size of the rachis and the size of the myrmecodomatium.

Ducke 1707, labelled by the collector as *T. myrmecophila*, is unfortunately sterile. In my opinion, it belongs to *T. cavipes*, although its scarcely myrmecophilous petiole bases and its subglabrous leaflets (except for the costa and the secondary veins above) seem to challenge this decision. The character of the foliage in general suggests *T. cavipes*.

The following common names are assigned to the Brazilian material of *T. cavipes:* "tachyzeiro", "tachi-preto", and "taxi".

7. TACHIGALIA **venusta** Dwyer, sp. nov. (T.: *Capucho 418!*).

Arbor 20–30 m.; ramuli terminales puberuli rotundati; stipulae (immaturae) 2–4 linearibus, segmentis 8 mm. longis; folia ad 32 cm. longa; petioluli graciles angulares torti puberuli, circ. 2–2.5 in medio lati, solitario basali myrmecodomatio inaequaliter elliptico, circ. 4 cm. longo, circ. 0.7 cm. lato; petioli plerumque subtumescentes subplano-convexi, ad 5 mm. longi, 1–2 mm. lati; foliola 3- vel 5-

jugata in toto sericeo-canescentia etiam ea vetusta tenui-coriacea plerumque inaequilateralia subelliptica vel ovato-oblonga (minimis ovatis), 6–15 cm. longa, ad 4.5 cm. lata, apice brevi-acuminata ultime obtusa plerumque inaequilateralia (rare cuneata), latere latiore plerumque subauriculato, costa supra prominula infra prominente basi, circ. 1.1 mm. lata, venis secundariis principalibus 6± argute ascendentibus, margine vix evidente; inflorescentiae patenti-paniculatae foliis breviores, rhachide centrale brevi, ad 5 cm. longo, circ. 2 mm. lato, puberulo torto basi, ramulis arcuato-ascendentibus subplano-convexis tortis, ad 7 cm. longis, racemis ad 5 cm. longis, bracteolis subulatis, ad 4 mm. longis; calyx receptaculi cupuliformis subparibus lateribus, latere longiore circ. 4 mm. longo, latere breviore circ. 3 mm. longo, pariete coriaceo crassoque, 0.7–1 mm. lato, extus minute pubescente intus farinoso (ova formicarum?); sepala inaequalia crassioria coriaceaque extus intusque minute canescentia oblongo-rotunda, 4–6 mm. longa, 4–4.5 mm. lata, apice obtusa, basi obtusa vel vix spathulata, ciliis longis albis irregularibus in medio corpore dispositis (nullis apice); stamina 10, antheris glabris oblongis, 7 filamentis subulatis, ad 9± mm. longis, ad 0.8 mm. latis, 3 latioribus crassioribus fusiformibus, circ. 6± mm. longis, ad 1.5 mm. in medio latis, omnibus basi intus fimbriato-ciliatis, ciliis crebris canescentibus saepe reflexis; stipes basi calicis eccentros, circ. 1.8 mm. longus, ovario in toto crebre canescente; fructus (maturi dehiscentesque) coriacei plani elliptici, 13–15 cm. longi, ad 4.5 cm. lati, apice obtusi et vix retusi, basi cuneati, semine solitario ala tenui lignosaque pericarpium in magnitudine aequante crebre striata.

BRAZIL: AMAZONAS: Manáos, Estrada Salles, *Ducke 1989* (NY); PARÁ: Tapajoz, Boa Vista, *Capucho 418* (F).

T. venusta is readily distinguished by its few-jugate leaflets, pubescent above and below, with the principal secondary veins averaging about 6 in number and curving in a characteristic arcuate pattern. The relatively thick axis of the inflorescence readily links it with *T. cavipes.*

8. TACHIGALIA PUBIFLORA Benth. in Hook. Jour. Bot. 2:94. 1890. (T.: *Schomburgk 43 (33?)!*).

Trees; terminal twiglets pubescent; stipules palmately or subpalmately segmented, the segments 3–5, the uppermost usually wider, linear-lanceolate, the lower linear-falcate, the entire stipule 6–16 mm. long, flat, pubescent; leaves up to 26 cm. long; petioles delicately canaliculate, tomentose, flattish to angular, subalate, 2–3 mm. wide at base, indented at point of petiolule-articulation; petiolules often tumescent, up to 6 mm. long; leaflets (2–)3- to 4(–6)-jugate, thin-coriaceous, drying dull gray-green above, dull golden-tan beneath, subequilateral, pubescent above, usually densely sericeous-tomentose below (older leaflets sometimes moderately pubescent), elliptic, up to 14 cm. long, 2–5.5 cm. wide, acuminate (acumen up to 1 cm. long), ultimately acute, subequilateral to obviously inequilateral at base, tapering acutely or obtusely at base, the costa subimmersed above, subprominent beneath, pubescent, the principal secondary veins 8–12, arcuate-ascending, subimmersed but obvious above, prominent beneath, the reticulations ultimately evanescent, the margin scarcely revolute, pubescent; inflorescence lax-paniculate, elliptic, the branches few (1–3), arcuate-ascending, up to 27 cm. long, the central rachis not strongly angular or squarrose below, 2.5–3 mm. wide at base, pubescent, the racemes narrow-pyramidal, usually 5–12 cm. long, up to 3 cm. wide at base; bracteoles linear-subulate, concave, auriculate at base, 0.4–1 cm. long, pubescent, often falcate at apex; buds inequilaterally obovate, about 1 cm. long at maturity; receptacle-cup inequilaterally cup-shaped, the wall 0.7± mm. thick, the longer side as seen in hemisection about 7 mm. long, the shorter side about 3 mm. long; sepals 5, stiff and thick, subpellucid, pubescent on both sides, the hairs silky, often more dense at base, oblong to oblong-rotund, 5–7 mm. long, 3.8–4(–6) mm. wide, obtuse at apex and base, the margin densely ciliolate, usually with small glandular bodies interspersed; petals 5, creamy-yellow (to orange, fide Abraham) in vivo, petaloid, hirsute within at the middle, glabrous on outside, obovate-oblong, 6.5–8 mm. long, 3.5–4.3 mm. wide, obtuse at apex, a fleshy keeled claw extending into corpus; stamens 10, the filaments of 7 linear-subulate, up to 15 mm. long, about 0.5 mm. wide at middle, densely pubescent at base on one side, filaments of 3 obviously thicker (usually wider at middle than at base), falcate, up to 9 mm. long, about 0.6 mm. wide in middle, sparsely hairy at base (one filament in one flower found to be entirely glabrous); stipe obviously eccentric, arising 2–3 mm. above base, short, about 2 mm. long, the ovary distinctly falcate, narrow-rectangular, about 5 mm. long, about 2 mm. wide, its central axis at apex almost at right angles to axis of receptacle-cup, the style linear-subulate, up to 14 mm. long, ciliate to middle; fruit green when ripening, purplish-gray at maturity, glaucous, flat, inequilateral, elliptic, often vaguely falcate, 6.5–11 cm. long, 1.9–2.5 cm. wide, the seed flat, brown, its position marked by a longitudinal ridge on each side of the wing, 2–3 mm. from margin, the wing acute to subobtuse at apex.

British Guiana: Cuyuni River, Oko Creek, *Tutin 339* (US); New River, Berbice Co., *Anderson 72* (US); Berbice, Rupununi Cattle Trail, *Abraham 253* (NY); Potaro River, Tumatumari, *Gleason 416* (NY, US); Demerara, *Jenman 5824* (NY), *6705* (NY); Mazaruni River, *Leng 267* (NY), *293* (NY); Kaieteur Plateau, Potaro River below Tukeit, *Maguire & Fanshawe 23483* (MO, NY, US); Caracara Creek, *Persaud 24* (F, NY); Essequibo River, *Sandwith 221* (NY, P); Essequibo, *Schomburgk 43 (33?)* (MO, P, US); without locality, *Schomburgk 322* (P).

Despite traditional acceptance of *T. pubiflora* I cannot distinguish it readily from typical *T. paniculata* Aubl. The strongest distinguishing characters are the persistent pubescence of the underside of the leaflets and the absence of myrmecodomatia. The former character, in light of my own observations on *T. paniculata*, *T. pubiflora*, and *T. rigida*, is very variable and should be employed with caution; the latter character is negative and as such is useful but scarcely convincing, especially when one considers that the majority of the collections of such a widely heralded myrmecophilous species as *T. paniculata* is also without myrmecodomatia. The shapes of the petioles of the two species, as seen in cross-section, are too variable to be employed as a critical distinguishing character. While the arcuate bending of the stipe and of the ovary is striking, nevertheless it is found in the variety *angustifolia* of *T. paniculata.* In general, the leaflets of *T. pubiflora* tend to be more elliptic, narrower, and more equilateral than in *T. paniculata;* in most collections the leaflets tend to taper more sharply at the base.

If the collection *Le Prieur 336* (not to be confused with the extant *Le Prieur 355*) from British Guiana is ever located, it may prove to be *T. pubiflora.* It is the type of *T. glauca* Tul. Both Bentham and Ducke mention that they have not seen the type.

On the Tutin collection *(339)* the common name, "Yawaridan", is recorded.

Krebs (Tropical Woods 13:28. 1928) has a description of the wood anatomy of *Persaud 24.*

9. TACHIGALIA PANICULATA Aubl. Hist. Pl. Guin. 1:372. 1775.

Tachigalia trigona Aubl. Hist. Pl. Guin. 1:372. 1775.
Tachigalia sericea Tul. in Arch. Mus. Nat. d'Hist. Nat. 4:163. 1844.
Tachigalia eriocalyx Tul. in Arch. Mus. Nat. d'Hist. Nat. 4:164. 1844.
Tachigalia angustifolia Miq. Sel. Stirp. 13. 1850.
Tachigalia alba Ducke, in Arch. Jard. Bot. Rio de Janeiro 3:92. 1922.
Tachigalia sulcata Benoist, in Bull. Mus. Nat. d'Hist. Nat. 31:469. 1925.
Tachigalia carinata Gleason, in Bull. Torrey Bot. Club 60:354. 1933.

Tree; ultimate twigs round in cross-section, glabrous to puberulent; stipules varying considerably according to age and habitat, often foliose, subcoriaceous, puberulent, segmented, the segments 2–7 (if 2 or 3 the uppermost segment larger), palmately disposed, the terminal segment broadly ovate to elliptic, up to 1.5 cm. long, the basal segments narrower, trapeziform to elliptic, acute; leaves up to 80 cm. long; petioles angular in cross-section, usually subtriangular, virgate to thick, often subcarinate, usually densely puberulent, usually expanded proximally where attached to twiglet, often with myrmecodomatia at base, these elliptic, 3–5 mm. long, puberulent to subglabrous; leaflets (2–)3–7(–9)-jugate, thin- to thick-coriaceous depending on exposure and habitat, inequilateral, subglabrous to microscopically puberulent above, subglabrous to densely puberulent below, often minutely furfuraceous below, the costa slender, prominulous above, subprominent beneath, pubescent above and below, the principal secondary veins 7–15, prominulous above and below, pubescent, acuminate or rarely acute (acumen up to 2 cm. long), ultimately obtuse or acute, the base obtuse to rarely subauriculate on wider side (rarely on both sides), the margin thin-callose; inflorescence lax-paniculate, often exceeding uppermost leaves, the central rachis rounded or angular in cross-section, subvirgate to stout, 2–3.5 mm. wide at base, often rugose with pedicel scars, the latter spirally arranged, the branches few to numerous, arcuate, the racemes narrow-pyramidal, up to 15 cm. long, up to 4 cm. wide at base (pressed condition), usually much shorter when basal flowers quickly deciduous, the bracteoles densely puberulent, falcate, subulate, 3–6 mm. long, acute; flowers long- to short-pedicellate; receptacle-cup inequilaterally cup-shaped to "pipe-bowl" shaped, the wall brittle-carnose to subcoriaceous, the longer side as seen in hemisection (3.5–)4–8 mm. long, the shorter side 2–4.5 mm. long, pubescent on outside, often ribbed, glabrous within; sepals 5, unequal, carnose, oblong, subrotund to subtriangular, the smaller 3.5–6 mm. long, 3–4 mm. wide, the larger 4.5–8 mm. long, 4–6 mm. wide, obtuse, the margin ciliolate with small red glandular bodies often interspersed; petals 5, thin, subequal in length, unequal in width, oblong to elliptic, 5–11 mm. long, 2–5.5 mm. wide, obtuse at apex, obtuse and often somewhat clawed at base, the hairs more or less restricted to the center or below middle; stamens 10, the filaments of two shapes and sizes, 3 (?) being thicker, 6–12 mm. long, 0.6–1 mm. wide in middle, 7 being 13–21 mm. long, 0.3–0.5 mm. wide in middle, all bearded at base, especially so within; the anthers oblong; stipe of pistil 2–3.5 mm. long, pubescent; ovary oblong, 3.5–4.5 mm. long, 1.8–2 mm. wide, uniformly appressed-hirsute, the type elongate, pubescent, especially below; fruit flat (mature fruit not seen), oblong, coriaceous; monospermate.

Locality unknown: *Barbier s. n.* (P).

FRENCH GUIANA: Kourou River, *Richard s. n.* (P); Cayenne, *Aublet s. n.* (F, MO, photo of type collection of *T. paniculata*); Cayenne, *Martin s. n.* (F); Maroni, *Mélinon 186* (F, P, US); without locality, *Le Prieur 355* (P).

BRAZIL: PARÁ: without specific locality, *Poeppig 3039* (F, syntype of *T. sericea*); Fordlandia, Tapajoz River, *Krukoff 1049* (NY); Belém, Agna Preta, *Ducke 1713* (F, NY, US); cataracts, Aripercuru, *Spruce s. n.* (NY); AMAZONAS: Santa Izabel, Rio Negro, *Ducke 326* (F, MO, NY, US); Manáos, Igarapé da Cachoeira Grande, *Ducke 2006* (NY, US); Ega, *Poeppig 2737* (F, type collection of *T. eriocalyx*); São Paulo de Olivença, near Palmares, *Krukoff 8252* (MO); São Paulo de Olivença, basin of Belém Creek, *Krukoff 8748* (F); Rio Negro, Barra, *Spruce 1677* (F, photo, NY, P, US); MATTO GROSSO: Tabajaza, upper Rio Machado, *Krukoff 1479* (NY, type collection of *T. carinata*).

PERU: LORETO: without locality, *Tessmann 6136* (F, frag.); Upper Amazonas, *Tessmann 3666* (F, frag.); Gamitanacocha, Rio Mazán, *Schuncke 26* (F, US); Mishuyacu near Iquitos, *Klug 1447* (F, NY, US); Iquitos, *Tessmann 3580* (NY); without specific locality, *Ule 6196* (F).

I have seen only a photograph of the Aublet type. It, together with most of the other material cited above, has narrow oblong leaflets which are moderately coriaceous. In general, *T. paniculata* is not readily confused with other species of the genus, with the exception of *T. pubiflora* Bentham (cf. the discussion following the description of the latter[12]).

Var. *a.* **angustifolia** (Miq.), Dwyer, stat. nov. (T.: *Kappler 1931!*).

Tachigalia angustifolia Miq. Sel. Stirp. 13. 1850.

Petioli saepe elongato-flabelliformes; foliola magna oblonga, circ. 20 cm. longa; calyx receptaculi extus costatus inequilateralis angusto-cylindricus, latere breve 4–8 mm. longo, latere longo 6–9 mm. longo, stipite ovarii angusto, 4–6 mm. longo.

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[12] Bailey (loc. cit.), in his work on *T. paniculata*, says the species is fairly common in the second growth of the forests of the Kartabo region (British Guiana). Apparently he sent samples to Col. David Prain, Director of Kew Gardens, who matched them with the solitary leaf of a Jenman collection, identifying the latter as *T. paniculata*. Inasmuch as Bailey describes the "hollow fusiform hypertrophy of the petiole" of his material, and since the well-known British Guiana species, *T. pubiflora*, lacks the basal hypertrophy of the petiole, we may assume that the species in question is *T. pubiflora*. If this be so, it establishes the fact that *T. paniculata* is found in British Guiana.

Surinam: Tafelburg Creek, Saramacca River, *Maguire 24896* (MO, NY, US, P); Marowyne River, *Kappler 1931* (P); Toekoemoetoe, *B. W. 5615* (MO, US); Toekoemoetoe, *Stahel 6340* (US).

French Guiana: Maroni, Ile Portal, *Sagot 1107* (P).

Two characters mark this variety: first, the very large oblong leaflets, and second, the very long stipe of the ovary. The leaflets are the largest found among the varieties of *T. paniculata,* as well as among all the species of the genus, and only one species of *Tachigalia* has an ovary stipe of comparable length, *T. pulchra* Dwyer.

Var. β. **sulcata** (Benoist) Dwyer, stat. nov. (T.: *Benoist 1574!*).

Tachigalia sulcata Benoist, in Bull. Mus. Nat. d'Hist. Nat. 31:469. 1925.

Foliola tenui-coriacea, ad 9 cm. longa, ad 3 cm. lata; petioli subvirgati; ovarium subsessile.

French Guiana: Gourdonville, *Benoist 1574* (P).

This variety is readily distinguished by its sessile ovary. No other species of *Tachigalia* possesses an estipitate ovary. In addition, the leaflets are thinner than in any other species with the possible exception of *T. agyrophylla.*

Var. γ. **comosa** Dwyer, var. nov. (T.: *Krukoff 8854!*).

Petala alba vel roseo-alba; corpora petalorum et filamenta staminum et ovaria dense comosa ciliis irregularibus elongatis ad 1.3 mm.

Colombia: amazonas: Trapecio Amazonico, Loreto-yuca River, *Schultes 8266* (US), *Schultes & Black 8360* (US).

Brazil: amazonas: São Paulo de Olivença, basin of Creek Belem, *Krukoff 8854* (MO).

The dense pubescence of the perianth parts enumerated above is unmatched by any other species of the genus, or in any other variety of *T. paniculata.* According to Schultes & Black's field-notes the vernacular name is "Ko-ne-kwa-cha-ku."

Var. δ. **alba** (Ducke) Dwyer, stat. nov.

Tachigalia alba Ducke in Arch. Jard. Bot. Rio de Janeiro 3:92. 1922. (Syntypes: *Ducke 17110, 17075!*).

Foliola plerumque lanceolata vel oblongo-lanceolata (minima ovata), circ. 10 cm. longa; petioli virgati; racemae plerumque elongatae, floribus parvis albis vel fulvis; calyx receptaculi parvus, ad 5 mm. longus; fructus oblongus, ad 12 cm. longus, ad 5 cm. latus.

Brazil: maranhão: Maracassumé River, *Froes 1942* (MO, NY); pará: Obidos, *Ducke 17110* (MO, photo, US); lower cataracts, Tapajoz, *Ducke 17075* (P, US); Boa Vista, Tapajoz River, *R. Monteiro da Costa 48* (F); Boa Vista, Tapajoz, *Capucho 348* (F); amazonas: Santa Izabel, Rio Negro, *Ducke 326* (F, MO, NY, US); Humaytá, Tres Casas, Basin Rio Madeira, *Krukoff 6326* (US); São Paulo de Olivença, *Ducke 937* (F, NY, US); Manaós beyond Flores, *Ducke 932* (MO, NY, US); mouth of Rio Embira, basin Rio Jurua, *Krukoff 4633* (MO, NY); acre: mouth of Rio Macauha, basin Rio Purus, *Krukoff 5586* (F, MO, NY, US).

It is with some hesitation that I reduce Ducke's species to the status of a variety. Its small receptacle-cup favors its retention as a distinct species. However, I am not able to find any other substantial character to support this retention; certainly the color of the flowers is variable (yellow to white); this seems to make the name "alba" a poor one[13]. The common names for the new variety are "Tachy Branco" and "Tachy Branco da Terre Ferme."

10. TACHIGALIA ULEI Harms, in Notizbl. Bot. Gart. Berlin 6:306. 1915. (T.: *Ule 6042!*).

Trees 5–15 m.; twiglets subterete or angular at apex, glabrous to subglabrous; stipules of 2–3 linear segments subequal in length (when two present), the longer 1.5–1.7 cm. long, the shorter 1.2 cm. long; petioles 6–10 cm. long, apparently angular in cross-section, about 2.5 mm. wide at base, the basal myrmecodomatia oblong, 3.2–3.8 cm. long, 0.5–0.8 cm. wide; petiolules twisted, about 2.5 mm. long, pubescent; leaflets (2?–)3- to 4-jugate, thin-coriaceous, subfalcate, oblong, 8–9 cm. long, up to 7.5 cm. wide, acuminate to ultimately very obtuse and minutely apiculate at apex, inequilateral at base, the costa prominent above and below, minutely pubescent, about 2 mm. wide at base, the principal secondary veins 8±, almost prominent above and below, arcuate-ascending, the reticulate areas lax above, the smallest of these evanescent below, the margin thin-callose, revolute; inflorescence lax-paniculate, corymbiform or somewhat funnelform, about 35 cm. long, the central rachis about 3 mm. wide, the branches usually arcuate-ascending, 12.5–22 cm. long; bracteoles not seen; receptacle-cup short, irregularly funnelform, the wall about 0.7 mm. thick, velutinous on outside, the shorter side as seen in hemisection about 3 mm. long, the longer side about 5 mm. long; sepals thick to subcoriaceous, somewhat woolly on both sides, ovate-oblong to oblong-rotund, 3.5–6 mm. long, 2.8–5 mm. wide, obtuse at apex and base, the margin densely ciliolate; petals subequal, petaloid (except thick at base), long-hirsute medianly within, appressed-hirsute on outside at base only, obtuse at apex, vaguely clawed at base; stamens 10, the filaments of 7 subulate, up to 14 mm. long, about 0.3 mm. wide in middle, bearded all around at base, the 3 remaining thickly subulate, 5–6.5 mm. long, about 0.9 mm. wide in middle, the hairs dense on one side below the middle; stipe short, thick, arising in the middle of receptacle-cup, the ovary narrow-rectangular in profile, about 5 mm. long, about 2 mm. wide, woolly-pubescent; fruit not seen.

BRAZIL: AMAZONAS: Rio Negro, *Ule 6042* (F, photo and frag., MO, photo).

T. ulei, described from a photograph and a few fragments of a leaflet and a flower, is readily distinguished by its few-jugate leaves with the costa of the leaflets prominent, its flat-topped funnelform inflorescence (in pressed state), and woolly sepals and ovary.

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[13] Ducke, in his original description, applies the adjective "albidus" to the cortex of the trunk and to the petals of the flowers. He does not make it clear whether he bases the specific name "alba" on both structures or on the petals alone. One of his collections *(932)*, labelled in his own handwriting as *T. alba,* bears the note that the flowers are yellow.

11. Tachigalia plumbea Ducke, in Bol. Técn. Inst. Agron. Norte Bras. 2:15. 1944. (T.: *Ducke 817!*).

Trees; terminal twigs subrotund in cross-section, minutely sericeous; stipules often persistent, foliose, bearing a solitary reduced basal segment, coriaceous, puberulent, oblong to ovate-oblong, 1.6–3 cm. long, 1–1.3 cm. wide, obtuse to subacute, the basal segment narrow falcate-lanceolate, up to 1.7 cm. long; leaves up to 30 cm. long; petioles thick, subrectangular in cross-section, pubescent, up to 10 cm. long, the basal myrmecodomatia 2.5–3.5 cm. long, about 0.6 cm. wide; petiolules swollen, plano-convex, pubescent, 4–7 mm. long, up to 3.5 mm. wide; leaflets 3- to 5-jugate, the terminal pairs often about twice the size of the basal pairs, the members of each pair somewhat unequal in length, coriaceous, minutely velutinous above and below, inequilateral, lanceolate, 7.5–20 cm. long, the larger leaflets about a third as wide as long, acuminate at apex, obtuse at base, the costa prominulous above, prominent beneath, 0.7–1 mm. wide at base, the principal secondary veins 7 to 12, arcuate-ascending, subprominulous to plane above, prominulous beneath, the ultimate reticulations evanescent to distinctly prominulous above, prominulous beneath; inflorescence lax-paniculate, the central rachis up to 14 cm. long, 0.35 mm. wide at base, the branches arcuate-ascending, contorted, triangular to angular in cross-section, up to 3 mm. wide at base, up to 15 cm. long, the terminal racemes narrow-pyramidal, about 6 cm. long, about 3 cm. wide at base, the rachis at base often rough with pedicel scars; bracteoles subulate, pubescent, about 5 mm. long; buds obliquely pyriform, about 1 cm. long at maturity; receptacle-cup caliciform, the wall very thick, 0.8–1.4 mm. thick, the longer side as viewed in hemisection 4.5–5.5 mm. long, the shorter side 2.5–3.5 mm. long, pubescent on outside, glandular-shiny and glabrous within, the internal cavity not spacious; sepals 5, 2 obviously smaller and thicker, all stiff and thick-subcoriaceous, densely velutinous on both sides, lanceolate, oblong to subrotund, 5–6 mm. long, 2.2–5.5 mm. wide, obtuse at apex and at base, the margin densely ciliolate; petals 5, pale-yellow, petaloid (except thick at base), long-appressed-hirsute within, glabrous on outside, obovate-rotund to obovate-oblong, up to 7 mm. long, about 4 mm. wide, obtuse at apex, often obviously clawed at base, the margin undulate; stamens 10, 7 filaments of which are more subulate and densely hairy at base on inside, the remaining 3 scarcely falcate to obviously so, as wide in the middle as at base, the basal hairs scattered, almost absent at point of attachment; stipe of pistil attached less than 1 mm. above the center of receptacle-cup, erect, stout, pubescent, about 2.5 mm. long, the ovary narrow-oblong, pubescent, the style apparently entirely glabrous; fruit not seen.

Venezuela: amazonas: Solano, Lower Casiquiare, *Llewelyn Williams 14734* (F).

Brazil: amazonas: Manáos, Estrada Campos Salles, *Ducke 24289* (P, US); Manáos, Pensador, *Ducke 817* (NY, US); Manaós near Cachoeira do Mindu, *Ducke 818* (MO, US).

12. TACHIAGALIA GRANDISTIPULATA Harms ex Pilg. in Notizbl. Bot. Gart. Berlin 6:304. 1915. (T.: *Ule 8399!*).

Trees; terminal twigs velutinous or subglabrescent; stipules large, foliose, segmented, with one large plane ovate-oblong segment 6–6.5 cm. long, and a smaller ovate basal segment 2.5 cm. long, 1.5 cm. wide; petioles thick (about 5 mm. wide in middle), often virgate at apex, 10–18 (–25) cm. long, bearing (at least in one leaf here) a basal myrmecodomatium 3.5 cm. long, about 0.75 cm. wide; petiolules tumescent, pubescent, 3.5–5 mm. long; leaves 4(–5)- to 6-jugate, the leaflets coriaceous, pubescent above and below, velutinous below, apparently ovate-oblong, up to 11 cm. long, up to 5 cm. wide, triangular- to long-acuminate to obtuse (?) at apex, the larger ones obtuse and not markedly inequilateral at base, the smaller ones obviously inequilateral, the costa prominulous above, more prominent beneath, velutinous, the principal secondary veins 8 to 10 (+?), arcuate-ascending, the ultimate reticulations fine but obvious under magnification, prominulous and lax below, often plane above; inflorescence lax-paniculate, up to 18 cm. long, the central axis subrotund in cross-section, about 0.25 cm. wide proximally, the branches strongly divergent to arcuate-ascending, up to 15 cm. long, 1.8–2.5 mm. wide in middle, usually averaging about 10 cm. in length, the terminal racemes 2–5 cm. long, 2± cm. in length on lower branches; bracteoles concave, pubescent, linear-subulate, 3–4 mm. long; buds silky-pubescent, narrowly obovate-oblong, about 8 mm. long; receptacle-cup short, inequilaterally funnelform, carnose, the wall about 0.6 mm. thick, the longer side as seen in hemisection 3–3.5 mm. long, the narrow side 1–1.5 mm. long, pubescent on outside, glabrous and apparently vaguely ribbed within; sepals 5, 2 smaller and thinner, carnose-subcoriaceous, concave, appressed-velutinous on both sides, oblong, obovate-oblong to oblong-rotund, 4.2–5 mm. long, 2.3–3 mm. wide, obtuse at apex and base, the margin densely ciliolate with red glandular bodies interspersed; petals petaloid, scattered-hirsute within medianly, glabrous on outside, obovate-oblong, 6–8 mm. long, 3–3.5 mm. wide, obtuse at apex, often clawed at base; stamens 10, the filaments unequal, essentially monomorphic, linear-subulate, 6–9 mm. long, 0.5–0.8 mm. wide at base, hirsute within for 3 mm. above base; stipe of pistil eccentric, arising about 1 mm. above base of receptacle-cup, pubescent, about 3 mm. long, 0.7 mm. wide in middle, suberect, the ovary densely velutinous, oblong-rectangular, the ovules seven; fruit not seen.

BRAZIL: AMAZONAS: Serra de Mairary, Surumu, Rio Branco, *Ule 8399* (F, photo, and frag., MO, photo).

Unfortunately, I have not seen a complete type-specimen. The only apparent distinguishing vegetative character is the very large stipules. Fortunately, flowers were available for dissection. These show a receptacle-cup which is "check-mark" shaped in profile, i.e. as seen in hemisection; the shorter side scarcely exceeds a millimeter in length. I have not observed a similar reduction of one side of the receptacle-cup wall in any of the other large-flowered species of *Tachigalia.*

13. Tachigalia myrmecophila (Ducke) Ducke, in Arch. Jard. Bot. Rio de Janeiro 3:91. 1922.

Sclerolobium myrmecophilum Ducke, in Arch. Jard. Bot. Rio de Janeiro 1:30. 1915. (T.: *Ducke 15659!*).

Large trees; twiglets round in cross-section, densely puberulent; stipules subcoriaceous, puberulent, of two segments, the upper one obliquely oblong-rotund, 1.5–2 mm. long, about 0.8 cm. wide, the basal segment shorter, narrow-elliptic, acute; leaves up to 30 cm. long; petioles subrotund, scarcely angular, densely puberulent, often moderately swollen from base to tip, the myrmecodomatia 2–3 cm. from base, elliptic, 2–3.5 cm. long, 1.5–2.5 cm. wide; petiolules slender, tumescent, 4–8 mm. long, puberulent; leaflets 2- to 4-jugate, sericeous-puberulent above and below (apparently even in mature leaflets), inequilateral, elliptic, oblong or ovate-oblong, 7–20 cm. long, 3–6 cm. wide, a little more than one-fourth as long as broad, obviously acuminate at apex, ultimately acute or obtuse, inequilateral, cuneate or obtuse at base, the costa prominulous to plane above, prominulous to prominent beneath, the principal secondary veins 8 to 10, prominulous above and below, arcuate-ascending, the ultimate finely reticulate; inflorescence lax-paniculate, the branches numerous, arcuate-ascending, 1.5–2 mm. wide in middle, conspicuously rugose with pedicel scars extending almost to base, the central floral axis exceeding (here) the side branches, all densely puberulent, the racemes shaped like a lizard-tail, some up to 14 cm. long, about 2.5 cm. wide at base, flowers soon deciduous, a few terminal ones persisting; bracteoles puberulent, concave, subulate, 5 mm. long, acute; receptacle-cup short and obliquely cup-shaped, the wall about 0.5 mm. thick, the shorter side as seen in hemisection 1.5–2 mm. long, the longer side 3.5–4 mm. long, pubescent on outside; sepals thin-subcoriaceous or thin-carnose, pubescent on both sides, oblong, often widely so, (2.8–) 3–5 mm. long, 2–4 mm. wide, obtuse at apex and base, occasionally broader than long; petals thin-carnose, petaloid, narrow-oblong, 4.5–5 mm. long, 1.5–2.2 mm. wide, distinctly to vaguely clawed, bearing a few scattered hairs on inside; stamens often dimorphic, some filaments measuring 0.4 mm. in width at middle, the others 0.6 mm., some 8–11 mm. long, some 5–8 mm. long; stipe of ovary short, 1–2 mm. long, subsigmoidal to erect, the ovary oblong, about 4 mm. long, the style short; fruit (fide Ducke) whitish-canescent, silky-pubescent, monospermate, 8–10 cm. long at maturity, 1.7–2 cm. wide, acute or obtuse at apex, shortly stipitate at base.

French Guiana: *Le Prieur s.n.* (P).

Brazil: pará: *Huber 646* (F, US); Rio Tapajoz, São Luiz, *Ducke 15819* (MO, photo, P, US, photo); Belém, *Ducke 15659* (F, photo and frag., MO, photo, US); Belém, Bosque Municipal, *Ducke 1706* (F, NY, US).

T. myrmecophila is readily confused with *T. paniculata*. However, its individuality is evident when one examines the flowers critically; the receptacle-cup is much smaller than in the Aublet species, the petals are only scattered-pubescent within, and the filaments of the stamens do not exceed 11 mm. in length. Unlike those of *T. paniculata* the leaflets of *T. myrmecophila* are apparently densely sericeous even in the mature state. The racemes bear a striking resemblance to those of our North American cimicifugas in their length and narrowness.

The unnumbered Le Prieur collection from French Guiana, while bearing immature flowers, certainly seems to have the foliage of typical *T. myrmecophila.*

"Tachy" and "Tachi-Preto" are two common names of the species. According to Hess and Record (Timbers of New World. p. 330. 1943), the wood of *T. myrmecophila* is very fetid in the fresh state; the bark is used locally in tanning.

14. TACHIGALIA FORMICARUM Harms, in Verhandl. Bot. Ver. Brandenb. 48:164. 1907. (T.: *Ule 6538!*).

Trees about 20 m. high; stipules plane, foliose, pinnate, the central segment elongate, narrow and inequilaterally oblong, about 2.2 cm. long, about 1 cm. wide, 2 basal segments on each side, linear, about 1.2 cm. long, acute; leaves up to 25 cm. long; petiole swollen at base, the basal myrmecodomatia 5–6 cm. long, about 1.2 cm. wide; petiolules scarcely swollen, about 5 mm. long; leaflets 4–6-jugate (the upper pairs larger and narrower), inequilateral, glabrous except for the veins, oblong, up to 16.5 cm. long, up to 4.5 cm. wide, triangular-acuminate, ultimately obtuse, obviously inequilateral and obtuse at base, the wider side subauriculate, the costa subimmersed to subprominulous above, prominent beneath, the principal secondary veins pubescent above and below, prominulous above, prominent beneath, the reticulations prominulous above and below, very conspicuous under magnification, ultimately distinct; inflorescence lax-paniculate, the branches divergent but not sharply ascending, almost the entire floral axis disposed as a myrmecodomatium, the axis about 9 mm. wide at base, about 5 mm. wide at apex, the lateral branches swollen, up to 22 cm. long, about 0.6 cm. wide at base, the racemes cylindrical, 5–7.5 cm. long, about 1.8 cm. wide at base and at middle; bracteoles coriaceous, pubescent, triangular, about 2 mm. long, about 1.8 mm. wide at base; buds rotund; receptacle-cup scarcely pedicellate, scarcely inequilateral, cupuliform, the wall coriaceous to carnose, about 0.4 mm. thick, puberulent on outside, glabrous and furfuraceous within (ant eggs?), the longer side as seen in hemisection 2.5–3 mm. long, the shorter side about 2 mm. long; sepals 5, small, concave, thick-subcoriaceous, pubescent on outside, puberulent and furfuraceous (ant eggs?) within, oblong to oblong-rotund, up to 4 mm. long, 2–3 mm. wide, obtuse at apex and base, the three largest subpellucid only on margins; petals subequal in size, petaloid, thick at base, glabrous on outside, densely hirsute within, the long scraggly hairs extending beyond margins, obovate-oblong to oblong, about 4 mm. long, about 2 mm. wide, obtuse at apex, obviously clawed at base; stamens 10, the filaments monomorphic, subulate, 4–6 mm. long, about 0.8 mm. wide in middle, the hairs long and scraggly on lower ⅖ on inside only; stipe of pistil shorter than cup, erect, the ovary suberect, velutinous, oblong, about 3.2 mm. long, about 1.5 mm. wide, the style eccentric, scattered-ciliate almost to apex; fruit not seen.

Peru: loreto: Tarapoto, *Ule 6538* (F, MO, photo); Aguaytia, *Weytkowski 34445* (MO).

The equilateral nature of the receptacle-cup as viewed in hemisection readily distinguishes *T. formicarum;* in fact undissected flowers bear a striking resemblance to those of *Sclerolobium.* However, the eccentric stipe suggests that the species belongs to the genus *Tachigalia.* The petals and sepals are of the same length, an unusual condition for the genus. The long scraggly hairs of the inner face of the petals and at the base of the stamens are longer than those of other species of *Tachigalia.* No other species of the genus has the filaments of the stamens so reduced in size. The close relationship between *T. formicarum* and *T. myrmecophila* is evidenced by their racemes; the latter resemble those of our North American cimicifugas.

The field-notes on the label of *Weytkowski 34445* are very enlightening: "Tree 12 m. high; flowers orange-yellow, anthers yellow, stalk green; flowers very fragrant; leaves very deep-green. Full of Tangarana ants which sting painfully."

15. Tachigalia polyphylla Poepp. & Endl. Nov. Gen. et Sp. 3:60. 1844. (T.: *Poeppig 2837!*).

Tachigalia poeppigiana Tul. in Arch. Mus. Nat. d'Hist. Nat. 4:168. 1844.

Terminal twiglets drying purple-black, smooth, rounded in cross-section, vaguely canaliculate; stipules not seen; leaves up to 25 cm. long; petioles virgate, pubescent, delicately canaliculate, up to 23 cm. long, about 0.2 mm. wide in middle, often with a myrmecodomatium about 7 cm. from proximal end which is 3–3.5 cm. long, 0.5–0.6 cm. wide; petiolules tumescent, 3–4 mm. long; leaflets 7- to 12-jugate, thin-coriaceous, subequilateral to obviously inequilateral, minutely pubescent above and below (at least on costa above), purplish-brown beneath, oblong-sublanceolate to narrow-oblong above, up to 9 cm. long, up to 2.5 cm. wide, acuminate at apex (acumen 0.8–1.2 cm. long), inequilateral at base, cordate-auriculate on wider side, often tapering narrowly on narrow side, the costa plane or prominulous above, prominent beneath, pubescent, the principal secondary veins 8±, prominulous above, subprominent beneath, the reticulations prominulous, lax, the margin scarcely differentiated, vaguely revolute; inflorescence paniculate, the floral axis about 3 mm. wide at base, usually about 0.8 mm. wide distally, velutinous, the branches 6–15 cm. long, about 0.15 mm. wide at base; bracteoles linear-subulate; pedicels about 1.5 mm. long; receptacle-cup small, thick-subcoriaceous, the wall about 0.5 mm. thick, pubescent on outside, glabrous within, inequilaterally oblong-rotund, obviously wider than long, the longer side as seen in hemisection about 3 mm. long, the shorter side about 1.5 mm. long; sepals 5, thin-carnose, pubescent on both sides, oblong, sublanceolate to rotund, 2.5–2.8 mm. long, 2–2.5 mm. wide, the veins evident, the margin ciliolate; petals 5, thin-pellucid, glabrous on outside, densely long-hirsute within, the hairs irregular, obovate-oblong to oblong, 3.2–4 mm. long, 2–2.2 mm. wide, obtuse at apex, obviously clawed at base, the veins evident; stamens 10, the filaments subequal, linear-subulate, 6–7.5

mm. long, about 0.35 mm. wide at base, the hairs densely lanose below middle, the anthers oblong-rotund, about 0.8 mm. long; stipe of ovary about 0.5 mm. long, slender, pubescent, the ovary oblong, sericeous, the hairs subappressed, elongate, about 2 mm. long, about 0.2 mm. wide, the style eccentric, the ovules about 8; fruit not seen.

BRAZIL: AMAZONAS: Fonteboa, *Ducke 20345* (US); Borba, Rio Madeira, *Ducke 23271* (US); Humaytá between Monte Christo and Santa Victoria on Rio Ipixuna, *Krukoff 7233* (MO, US); Ega, *Poeppig 2837* (P), *Poeppig s.n.* (F, frag.).

T. polyphylla is one of the most easily recognized species of the genus. It is readily distinguished from *T. multijuga* Benth., the only other species of the genus with numerous pairs of leaflets. The very small flowers with very short receptacle-cups suggest *Sclerolobium*. However, the eccentric stipe and inequilateral receptacle-cup exclude them from this genus.

Coupled with the very small flowers and characteristically shaped receptacle-cup are other characters of note: leaflet pairs are occasionally alternate; the petals are densely hairy with long irregular hairs; and the filaments of the stamens are lanose at the base.

There is a fine plate *(t. 265)* of *T. polyphylla* in Poepp. & Endl. Nov. Gen. et Sp. (3:60. 1844). The common name of *T. polyphylla,* according to Ducke's label, is "Tachy."

16. TACHIGALIA AGYROPHYLLA Ducke, in Bol. Técn. Inst. Agron. Norte Bras. 2:14. 1944. (Syntypes: *Ducke 936, Ducke 937!*).

Large trees; terminal twiglets round in cross-section, virescent and velutinous; stipules not seen; leaves up to 29 cm. long; petioles up to 21 cm. long, virgate, virescent and velutinous, angular in cross-section, about 0.15 cm. in middle, with a myrmecodomatium about 2 cm. above point of articulation, oblong, 2.5–3 cm. long, about 1 cm. wide; petiolules slender; leaflets 6- to 7-jugate, stiff-chartaceous, inequilateral, lustrous, velutinous above and below, ovate-elliptic to elliptic, the lower pairs smaller than upper pairs, 7–11.5 cm. long, 2.5–3.8 cm. wide, gradually acuminate at apex (acumen up to 1 cm. long), obtuse and minutely apiculate, inequilateral at base, the narrow side obtuse to acute, the wider side in the larger leaflets obtuse to subauriculate, the costa plane above, about 1 mm. wide at base, prominent beneath, the principal secondary veins 4 to 5 per side, angular-ascending, at least the proximal part soon obviously arcuate-ascending, prominulous and conspicuous above, prominent beneath, the intermediate and ultimate reticulations prominulous, evident above and below; inflorescence densely branched, the panicle lax, the floral axis up to 18 cm. long, about 0.3 cm. wide at base, smooth, velutinous, delicately canaliculate, the branches arcuate to sharply ascending, 7–10 cm. long, about 0.11 cm. wide at base, floriferous almost to base; bracteoles concave, subcarinate at base, pubescent, subulate, about 5 mm. long, acute; pedicel about 3.5 mm. long, pubescent; receptacle-cup inequilaterally caliciform, tapering gradually toward base, carnose, the wall about 0.5 mm. thick, the longer side of the cup as seen in hemisection about 3.5 mm. long, the shorter side 2.5–2.8 mm. long; sepals 5, thin-carnose, often stiffly so, velutinous on both sides, the 2 smaller ovate-rotund, usually wider than long, about 3 mm. long, about 3.5 mm. wide, tapering obtusely at apex, the 3 larger ones rotund to oblong-rotund, about 4.5 mm. long, about 4 mm. wide, the marginal veins evident, the margin ciliolose; petals 5, petaloid, concave, glabrous on outside, densely irregular-hirsute within almost to margin, with hairs scattered below middle on outside, more numerous at base, oblong to obovate-oblong, 4.2–5 mm. long, 3–3.5 mm. wide, obtuse to rounded at apex, short-clawed at base, the veins striate; stamens 10, apparently all more or less similar in shape and width, subulate, some bent falcately, 7–9 mm. long, 0.6–0.8 mm. wide at base, the hairs on inner side only below middle, more dense at apex of pubescent area; stipe of pistil thick, arising about 0.5 mm. from base of receptacle-cup, the ovary densely hairy, about 4 mm. long, about 1.7 mm. wide, curved falcately, the stigma apparently bifid; fruit not seen.

Brazil: amazonas: Rio Negro, Paraná de Anavilhana between the mouths of the Araras and Cuieras Rivers, *Ducke 936, 937* (F, MO, NY).

T. agyrophylla is marked by a number of distinguishing characters: the leaflets are few, chartaceous in texture, usually ovate-elliptic in shape, with relatively few secondary veins arising abruptly. The inflorescence is many-branched with very slender branches; the flowers are very small with the receptacle-cup very reduced, the petals are densely pubescent almost to the margins, the stamens are submonomorphic, and the stigma bifid.[14] The majority of these characters is found in *T. formicarum* and *T. polyphylla* and suggest that the trio is closely related.

17. Tachigalia rusbyi Harms, in Engl. Bot. Jahrb. 33, Beibl. 72:20. 1903. (T.: *Rusby & Squires 127!*).

Trees up to 40 m. high; terminal twigs essentially rounded, delicately canaliculate, puberulent; stipules not seen; petioles conspicuously angular, triangular in cross-section, with a myrmecodomatium about 3 cm. long and 0.9 cm. wide, located below attachment of proximal pair of petiolules, carinate and canaliculate, nodose at petiolule-attachment, 15–25 cm. long, about 0.5 cm. wide in middle, puberulent; petiolules plano-convex, tumescent, up to 1 cm. long, about 0.4 cm. wide in middle, puberulent; leaflets (4–)6- to 7-jugate, stiff-coriaceous, scattered-puberulent, drying purplish-brown above, narrow-oblong to widely oblong, inequilateral, 10–23 cm. long, 3–7 cm. wide, acuminate, cuneate to obtuse, often vaguely auriculate at base on wider side, the costa plane to prominulous above, often densely puberulent, 1–2 mm. wide at base, prominent beneath, the principal secondary veins 8 to 12, prominulous above, subprominent beneath, the ultimate reticulations conspicuous to evanescent above, conspicuous beneath, the margin

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[14] Whether the bifid stigma represents a worth-while distinguishing character is questionable. It is difficult to observe. I believe that I have observed it in flowers of other species of *Tachigalia*.

thin-callose; inflorescence lax-paniculate, exceeding the leaves, the floral axis and branches very angular, basally and medianly rugose with pedicel scars, the secondary branches up to 22 cm. long, 2–8 mm. wide at base, the racemes up to 7 cm. long; bracteoles densely pubescent, subulate, 4–6 mm. long, acute; receptacle-cup and its short pedicel inequilaterally caliciform, the wall stiff-carnose to coriaceous, 0.3–0.5 mm. thick, the longer side as seen in hemisection 3.5–5 mm. long, the shorter side 2–2.5 mm. long; sepals thin-carnose, often thicker at the base, the two smaller ones less pellucid, minutely pubescent on both sides, the remaining three often minutely punctate, concave, oblong-rotund to narrow-oblong, 3.5–5 mm. wide, obtuse at apex and base, the margin densely ciliolate, the veins evident on the margin in the largest ones; petals pale yellow or sulphur-yellow, petaloid, laxly hirsute within, often minutely rugose, oblong, 5–6 mm. long, 2–3 mm. wide, obtuse to subacute at apex, usually distinctly clawed at base; filaments of stamens subulate, 3 of these thicker in middle, 0.6–0.7 mm. wide, subfalcate to erect, 6–10 mm. long, the other 7 more slender, 0.2–0.5 mm. wide in middle, suberect, scarcely exceeding the thicker filaments in length, all pubescent at base, often only on inner face; stipe of ovary conspicuous, 2–3 mm. long, usually barely exceeding the shorter side of cup, arising abruptly near middle of cup, the ovary oblong, densely pubescent, 3.5–4 mm. long, the style 6–8 mm. long; fruit not seen.

British Guiana: Cuyuni River, Akarabice Creek, *Tutin 440* (US); Bartica-Potaro Road, *Tutin 201* (US).

Venezuela: Lower Orinoco, Santa Catalina, *Rusby & Squires 127* (MO, NY, US); bolívar: Río Caroní, Arabayen, Guayana, *Cardona 1654* (NY, US).

Brazil: amazonas: São Paulo de Olivença, *Froes 20689* (NY).

Several characters serve to distinguish *T. rusbyi:* the markedly nodose and triangular (in cross-section) petioles, and the small flowers. The petals of the flowers are often rugose and the filaments of the stamens subequal in length. The calyx-cup assumes the form of an inequilateral chalice when viewed in profile together with the pedicel.

Cardona 1654 possesses remarkably narrow leaflets considering their length; its petiole gives evidence of tumescence along its length, as in *T. formicarum* Harms. I have included the immature *Froes 20689* in *T. rusbyi* primarily because of the nodosity of its petioles, the conspicuous ultimate reticulations of the leaflets, the carinate tips of the branches, and in the general habit of the branches of the inflorescence.

In British Guiana *T. rusbyi* is known by the common name "Yawarddan", while in Brazil by "Taxi."

18. Tachigalia **pulchra** Dwyer, sp. nov. (T.: *Cardona 1180!*).

Arbores; ramuli terminales dense argenteo-sericei canaliculati torti; stipulae non visae; folia ad 25 cm. longa; petioli minute carinati puberuli angulati, ad 14 cm. longi, circ. 3.5 mm. in medio lati; petioluli marcescentes subtumescentes, circ. 3 mm. longi; foliola 6-jugata tenui-coriacea supra subglabrescentia (praeter costam) infra minute puberula oblonga, ad 14 cm. longa, ad 3.8 cm. lata, apice acuta (ultime mucronata) basi obtusa, venis secundariis principalibus 10± supra planis infra prominulis, marginibus vix revolutis; inflorescentiae paniculatae dense puberulae, rhachide centrale ad 16 cm. longo, ramis paucis divergentibus angulatis gracilibus (circ. 1.5 mm. in medio latis) nodosis (cicatricibus pedicellorum), racemis dense floriferis angusto-pyramidalibus, ad 8 cm. longis, circ. 2 cm. latis, floribus inferioribus mox deciduis; bracteolae dense argenteo-puberulae lato-subulatae, ad 2 mm. longae, acutae mox deciduae; calyx receptaculi parvus oblique cupuliformis, pariete crasso-coriaceo, circ. 1.2 mm. lato extus pubescente intus glabro latere longiore circ. 3 mm. longo, latere breviore circ. 2 mm. longo; sepala 5 tenui-carnosa extus minute lanosa concava oblonga, circ. 4 mm. longa, 2–2.5 mm. lata, apice obtusa marginibus dense ciliolatis; petala 5, tenui-carnosa, corpore basale crassiore intus sparse pubescentia ciliis longis irregularibus, oblonga vel obovato-oblonga, 4.8–5 mm. longa, circ. 3 mm. lata, obtusa vix basi spathulata; stamina 10, filamentis duobus generibus, 3 brevioribus crassioribus, circ. 5 mm. in medio latis, 7 gracili-subulatis, ad 10 mm. longis, 0.4–0.6 mm. latis; stipes ovarii longus, 3–8 mm. longus, circ. 0.7 mm. latus, curvatus, ovario compresso-oblongo vel subtrapeziforme, 1–2 mm. longo, circ. 1.2 mm. lato in toto pubescente, stylo breve, circ. 7 mm. longo; fructus non visus.

VENEZUELA: BOLÍVAR: Alto Rio Paragua, *Cardona 1180* (US).

T. pulchra is recognized readily by its very long-stipitate ovary which is strikingly different in shape from that of any other species of the genus. The new species is obviously related to *T. rusbyi;* in fact, the foliage of the two species is apparently indistinguishable. The vernacular name of *T. pulchra* is "Tachi-yék (Arekuna)."

19. TACHIGALIA TESSMANNII Harms, in Notizbl. Bot. Gart. Berlin 9:967. 1926. (T.: *Tessmann 4753!*).

Trees 15 m. high; twiglets smooth, minutely pubescent, often minutely canaliculate; stipules not seen; leaves up to 35 cm. long; petioles virgate, up to 25 cm. long, about 0.8 mm. wide in middle, with a solitary myrmecodomatium at base which is oblong, about 3 cm. long, about 1 cm. wide; petiolules short; leaflets 6-jugate (the pairs 4–5 cm. apart in the middle of petiole), thin, chartaceous to subcoriaceous, up to 17 cm. long, up to 6.5 cm. wide, subequilateral to obviously inequilateral, apparently long-acuminate, obtuse and often auriculate at base, inequilateral, the costa pubescent above and beneath, more prominent beneath, angular in cross-section, the principal secondary veins 8±, prominulous above, prominent beneath, arcuate-ascending, reticulations more prominent above; inflorescence lax-paniculate, ovate-rotund, shorter than uppermost leaves, about 15 cm. long, about 14 cm. wide, the branches 5–8.5 cm. long, usually sharply ascending, larger ones often suberect, the racemes 5 cm. long, up to 1.5 cm. wide at base; bracteoles subulate, concave, swollen at base, pubescent; buds narrow-obovate, about 6.5 mm. long, scarcely pedicellate; receptacle-cup inequilaterally urceolate, one side as seen in hemisection 3.5–4 mm. long, the other 2.4–2.6 mm. long, the wall about 0.4 mm. thick, pubescent on outside; sepals 5, 2 of which are smaller and thick, all stiff-coriaceous, usually rugose on outside, ovate-oblong to rotund, 3–3.5 mm. long, 2–2.5 mm. wide, the margins of larger sepals usually subpellucid; petals 5, subequal, 3–4 mm. long, about 2 mm. wide, obovate-oblong, oblong to ovate, usually obtuse, rarely subacute at apex, obtuse to short-spatulate at base, obviously rugose under magnification (especially in middle), glabrous on outside, scattered-hirsute within, the hairs long and subappressed, the principal veins 3, subflabellate-ascending, the margin often irregular; stamens 10, the filaments subequal, subulate, 5–6.5 mm. long, 0.35–0.5 mm. wide at base, densely bearded on one side at base, the hairs divergent-hirsute, the anthers oblong to rotund, about 1 mm. long; stipe of pistil short, about 1.5 mm. long, attached above the middle of the cup on longer side as seen in hemisection, the ovary suberect to subarcuate, densely pubescent, oblong, about 3 mm. long, the style short; fruit not seen.

PERU: LORETO: Puerto Velendez, Pongo de Manseriche, *Tessmann 4753* (MO, photo, NY).

T. tessmannii is readily recognized by its widely spaced leaflets borne on a virgate petiole, its minute flowers with the petals rugose and markedly 3-veined, the stamens spreading radiately at anthesis, and the filaments monomorphic.

20. TACHIGALIA MACROSTACHYA Huber, in Bol. Mus. Goeldi (Para.) 5:387. 1909. (T.: *Ducke 9030!*).

I have elected not to describe this species in a formal manner inasmuch as I have not seen the type material. Huber's description, considerably condensed, is as follows: twiglets and rachis of the inflorescence swollen and myrmecophilous; leaflets, 4- to 5-jugate, ovate-oblong (10–20 × 5.5–6.5 cm.), secondary veins "transversalibus", margin bullate; rachis of inflorescence apparently subglabrous, about 8 mm. thick; receptacle-cup disciferous, about 9 mm. long; stamens 15 (–16–19), the filaments varying considerably in length.

If this plant belongs in *Tachigalia* it is certainly a very distinct species. In no other species of the genus have I observed a rachis of the inflorescence more than 4 mm. thick, a bullate leaf-margin, stamens in excess of 11, and transverse secondary veins. The generalized swelling of the petioles mentioned by Huber is limited to three species of *Tachigalia* examined: *T. formicarum* Harms, one collection of *T. rusbyi* Harms, and in certain collections of *T. cavipes* (Spruce ex Benth.) Macbr.

Assuming that *T. macrostachya* is a valid species, its large and glabrous leaflets and large receptacle-cup suggest a possible relationship with the *T. longiflora* and *T. catingae* complex.

VENEZUELA: AMAZONAS: Rio Mapuera, *Ducke 9030.*

21. Tachigalia ptychophysca Spruce ex Benth. in Mart. Fl. Bras. 15^2:229. 1876. (T.: *Spruce 2644!*).

Twiglets drying deep chocolate-brown, minutely pubescent, vaguely canaliculate; leaves up to 45 cm. long; stipules not seen; petioles virgate, up to 30 cm. long, subplane, delicately canaliculate, puberulent, often swollen about 2 cm. above the point of petiolule-attachment into an oblong myrmecodomatium about 2.5 cm. long, about 0.5 cm. wide; petiolules 4–5 mm. long, 1–2 mm. wide, often twisted; leaflets 6-jugate (pairs 2–3 cm. apart), stiff, coriaceous, drying dull golden-green when pubescence sericeous, the older and less pubescent ones deep purple above and chocolate beneath, equilateral, elliptic, 7.5–16 cm. long, up to 6.5 cm. wide, acuminate, ultimately obtuse, tapering cuneately at base, the costa apparently plane above, prominent beneath, 0.7 mm. wide at base, the prominent secondary veins arising from the lowermost third of the lamina, one large vein on one side, two on the other, the outermost of the two quickly disappearing at margin, all veins more prominent beneath, the reticulations subevanescent to obviously prominulous, the margin subrevolute; inflorescence terminal, lax-paniculate, the central floral axis ferrugineous, up to 15 cm. long, the principal branches obviously arcuate-ascending; bracteoles widely subulate, scarcely concave, incurved, pubescent, about 7 mm. long, about 0.3 mm. wide at base; buds obliquely clavate; receptacle-cup brittle-coriaceous, the wall about 0.7 mm. thick, inequilaterally urceolate, ribbed and minutely pubescent on outside, furfurcaceous within, concave, subcoriaceous, oblong to subrotund, often broader than long, 3.5–6 mm. long, 3–4.2 mm. wide, obtuse at apex, the margin often very thin, ciliolate; petals concave, all subcarinate in middle, appressed-hirsute within, 6–7 mm. long, 4–5 mm. wide, acute to obtuse at apex, subclawed to spatulate at base, the marginal veins often striate; stamens 10(–11), the filaments of 3(–4) shorter and thicker and falcate, 7–8 mm. long when stretched, wider and geniculate above middle, pubescent below middle, the remaining 7 subulate, 7–11 mm. long, pubescent at very base; stipe of pistil attached in middle of lower half of cup, about as long as or longer than shorter side of receptacle-cup, the ovary narrow-oblong, about 4 mm. long, about 1.6 mm. wide, the ovules 10 to 15; fruit not seen.

Brazil: amazonas: Panuré, Rio Vaupés, *Spruce 2644* (F, photo and frag., P); without locality, *Spruce 2022* (P, only half of sheet).

This is the simplest of all of the species of *Tachigalia* to recognize. In no other species of the genus are there as few as one or two secondary veins on each side of the lamina.

The great variation in the pubescence of the young and old leaflets seems to substantiate Bailey's observation on *T. paniculata*.[15] The confusing status of the Spruce collection *2022*, deposited in Paris, has been discussed following the description of *T. multijuga*. The widely subulate bracteoles of *T. ptychophysca* are not found in any other species of the genus with bracteoles of comparable length.

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[15] Bailey, I. W. Bot. Gaz. 75:27–41. 1922.

22. **Tachigalia versicolor** Standley & Williams, in Ceiba 3:27. 1952. (T.: *Allen 5594!*).

Trees up to 36 m.; terminal twiglets almost smooth, delicately canaliculate, densely pubescent; stipules not seen; leaves up to 50 m. long; petioles subrotund in cross-section, delicately ridged, up to 32 cm. long, about 3.5 mm. wide in middle, densely puberulent; petiolules puberulent, 3–4 mm. long; leaflets 7-jugate, the members of each pair usually very unequal, thin-coriaceous, subglabrous above (except costa), puberulent below, the hairs usually scattered, oblong, up to 20 cm. long, up to 7 cm. wide, subacuminate and ultimately obtuse above, inequilaterally cordate at base, the costa slender and prominulous above, the secondary veins 10± in larger leaflets, slender and subplane above, prominent beneath, arcuate and not sharply ascending, the ultimate reticulations subevanescent above, evident beneath, the margin slender-callose; inflorescence lax-paniculate, about 40 cm. long, subcorymboid (in pressed condition), the branches upright-whorled, 1–3 cm. apart, gracefully arcuate-ascending, up to 20 cm. long, the central rachis above uppermost branches 13 cm. long, about 0.3 mm. wide at base; bracteoles not seen; flower-buds inequilaterally obpyriform and about 9 mm. long at maturity, pinkish-lavender in vivo when unexpanded; receptacle-cup widely and inequilaterally urceolate, the longer side as seen in hemisection 4–5 mm. long, the shorter side 2–3 mm. long; the wall coriaceous, about 1 mm. thick; sepals 5, thick-carnose (2 much reduced and very carnose), pubescent on both sides, ovate-oblong to oblong-rotund, 5–7 mm. long, 3–5 mm. wide, obtuse at apex, the margin ciliolate with minute glandular excrescences interspersed; petals 5, subcarnose, obviously carnose at base, subappressed-hirsute within medianly, glabrous on outside, obovate to widely obovate, 8–8.5 mm. long, 4 mm. wide, obtuse, rarely acuminate, usually deeply lobed, obviously clawed at base, the veins substriate; stamens 10, the filaments pubescent at base (except one entirely glabrous) on inner side, 6 or 7 filaments more slender at base, 0.6–0.7 mm. wide, up to 11 mm. long, the remainder usually rectangular in cross-section at base, up to 7 mm. long, the anthers glabrous, up to 2.8 mm. long; stipe of ovary thick, about as wide proximally as distally, about 3 mm. long, the ovary rectangular, 5 mm. long, 2.5 mm. wide, entirely pubescent, the hairs partially disposed in obvious longitudinal rows, the ovules about 15; fruit not seen.

Costa Rica: puntarenas: upper Río Piedras Blancas, vicinity Río Esquinas, *Allen 5594* (MO).

T. versicolor, the only extra-South American species of *Tachigalia,* is readily distinguished by the following characters: the members of the pairs of leaflets are strikingly different in size; the receptacle-cup is widely and inequilaterally urceolate; one filament of the stamens is entirely glabrous; the anthers are very large; and the ovary has its hairs disposed in longitudinal rows.

I am certain from numerous dissections of tachigalias that the striate pubescence of the ovary is not found in any other species of the genus. Only in the flowers of one collection of *T. pubiflora, Persaud 24,* did I observe another entirely glabrous solitary filament of the stamen.

In the original description of *T. versicolor* the fruit is described as: ". . . . strongly compressed, narrow-oblong, 14–15 cm. long, round and apiculate at apex, the seed strongly compressed, cuneate-obovate, 3.3 cm. long, 2 cm. wide, narrowly marginate." Unfortunately I did not see the fruit.

Excluded Species

I have omitted *Tachigalia grandiflora* Huber (Bol. Mus. Goeldi [Para.] 5:388. 1909), based on a sterile collection of Ducke *(8965)* made at the Mapuera River, Brazil, below the "cataracts do Pataua." Unfortunately, I have not seen the sterile (?) type material.

In studying a collection of Riedel *(804)* I discovered that it is not *Tachigalia* but *Dicymbe* Spr. ex Benth. Therefore:

Dicymbe **psilophylla** (Harms) Dwyer, comb. nov.

Tachigalia psilophylla Harms, Bot. Gart. Berlin Notizbl. 6:305. 1915.

Brazil: bahia: without specific locality, *Bondar s. n.* (F); state ?: Esperanaca, *Riedel 804* (F, photo and frag. of type, collection of *Tachigalia psilophylla*).

The glabrous to subglabrous filaments of the stamens (fide Harms), the large reniform stipules, and the very long cigar-shaped fruits leave no doubt that this is a species of *Dicymbe.*

Index to Exsiccatae

SYSTEMATIC INDEX

Roman type indicates accepted, pre-existing names; *italics* indicates synonyms; **bold face** indicates novelties.

Explanation of Plate

PLATE 9

Hemisections (except for *T. paniculata* var. *comosa*) of the receptacle-cups of species of *Tachigalia* showing the length and location of the stipe of the pistil. Occasionally the ovary and the style have been included. The drawings are arranged according to the sequence of the species in the paper; *T. macrostachya* alone has not been included.

Fig. 1. *T. longiflora: Ducke 24291*, × about 5.
Fig. 2. *T. catingae: Ducke 35421*, × about 5.
Fig. 3. *T. multijuga: Spruce 2022*, × about 5.
Fig. 4. *T. rigida: Ducke 35423*, × about 5.
Fig. 5. *T. bracteolata: Martin s. n.*, × about 5.
Fig. 6. *T. cavipes: Krukoff 6816*, × about 5.
Fig. 7. *T. venusta: Ducke 1989*, × about 5.
Fig. 8. *T. pubiflora: Schomburgk 43 (33?)*, × about 5.
Fig. 9. *T. paniculata: LePrieur 355*, × about 5.

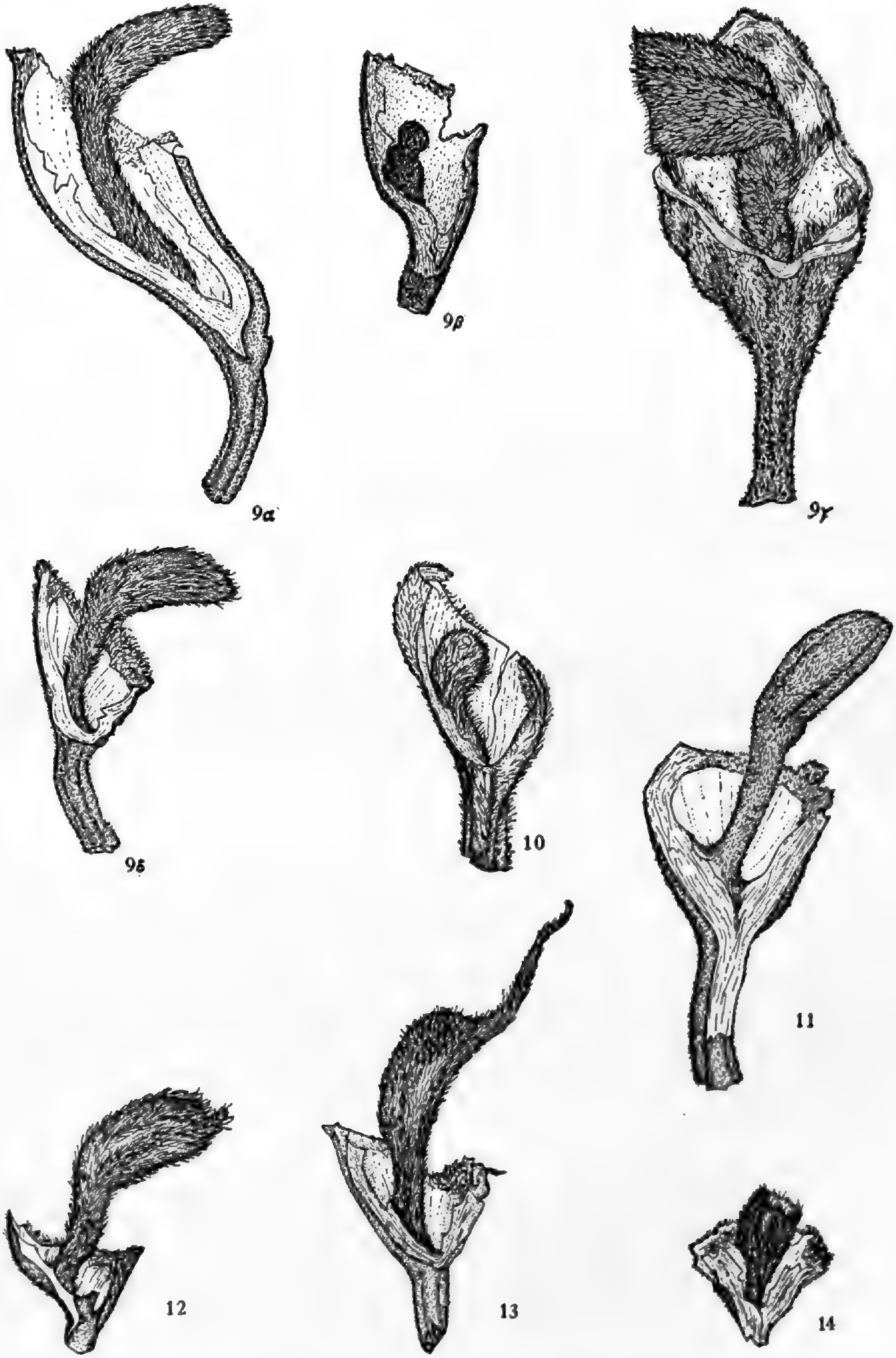
DWYER—TROPICAL AMERICAN TACHIGALIAS

Explanation of Plate

PLATE 10

Fig. 9. *T. paniculata:*
  - α. *angustifolia: B. W. 5615,* × about 5.
  - β. *sulcata: Benoist 1574,* × about 5.
  - γ. *comosa: Krukoff 8854,* × about 5. Top view of entire receptacle-cup, including stipe and part of ovary.
  - δ. *alba: Ducke 17075,* × about 5.

Fig. 10. *T. ulei: Ule 6042,* × about 5.
Fig. 11. *T. plumbea: Ducke 818,* × about 5.
Fig. 12. *T. grandistipulata: Ule 8399,* × about 5.
Fig. 13. *T. myrmecophila: Ducke 1706,* × about 5.
Fig. 14. *T. formicarum: Ule 6538,* × about 5.



DWYER—TROPICAL AMERICAN TACHIGALIAS

Explanation of Plate

PLATE 11

Fig. 15. *T. polyphylla: Krukoff 7233,* × about 5.
Fig. 16. *T. agyrophylla: Ducke 936,* × about 5.
Fig. 17. *T. rusbyi: Rusby & Squires 127,* × about 5.
Fig. 18. *T. pulchra: Cardona 1180,* × about 5.
Fig. 19. *T. tessmannii: Tessmann 4753,* × about 5.
Fig. 21. *T. ptychophysca: Spruce 2644,* × about 5.
Fig. 22. *T. versicolor: Allen 5594,* × about 5.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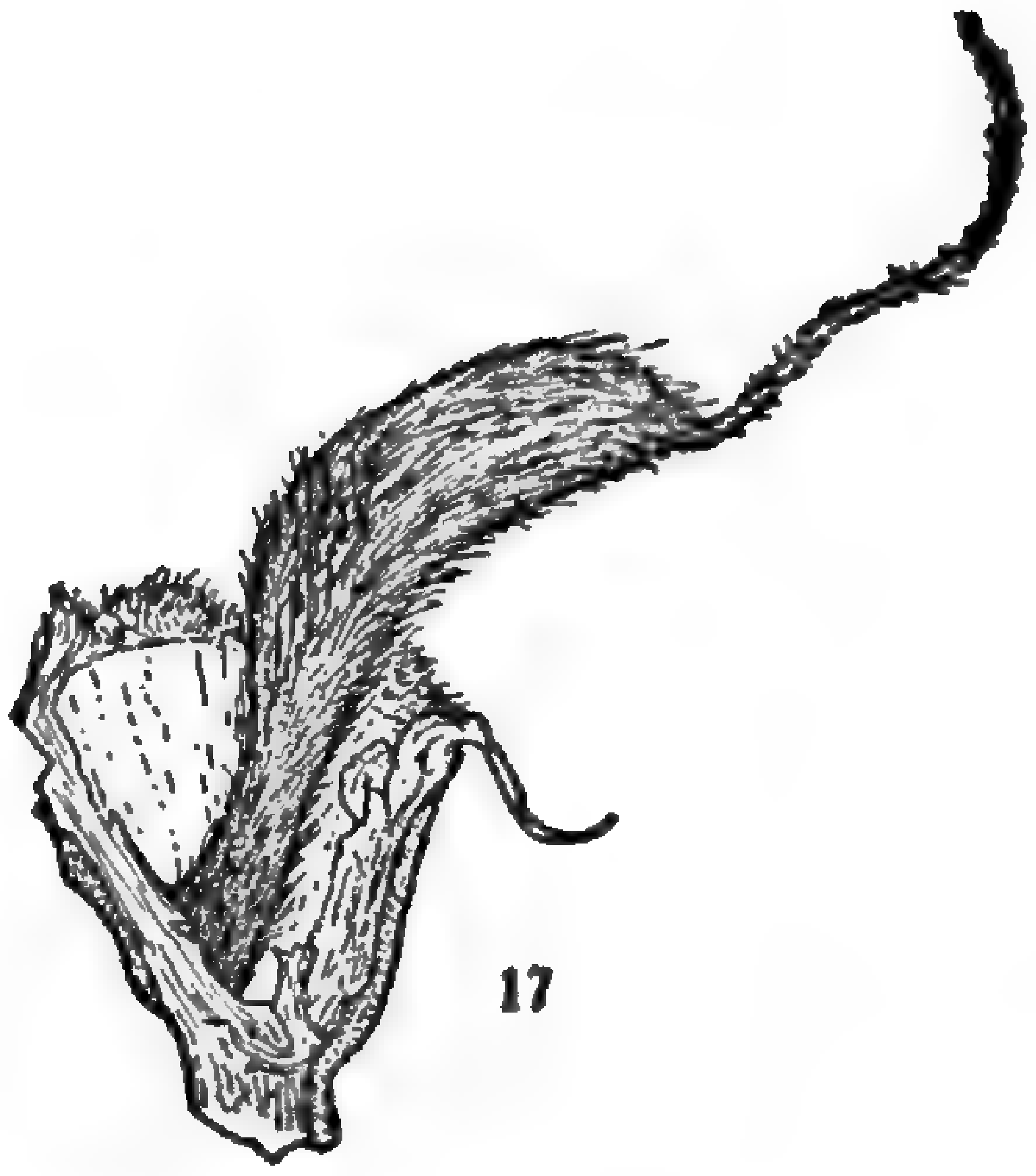
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DWYER—TROPICAL AMERICAN TACHIGALIAS

A CORRECTION IN ASCLEPIAS

ROBERT E. WOODSON, JR.

Professor G. Neville Jones, of the University of Illinois, has called my attention to an error in my recent revision of *Asclepias* (Ann. Mo. Bot. Gard. 41:1–211. 1954), which unfortunately results in still a second error. I am grateful for Prof. Jones's interest, and only wish that I might have profited from it before publication!

Asclepias lanuginosa Nutt. Gen. 1:168. 1818, was omitted from the bibliography of the species treated by me (loc. cit. p. 175) as *A. nuttalliana* Torr. in Ann. Lyc. N. Y. 2:218. 1828, and obviously has priority of publication. All references to *A. nuttalliana* Torr. should be changed to read *A. lanuginosa* Nutt.

Asclepias otarioides Fourn. in Ann. Sci. Nat. Bot. Ser. VI, 14:373. 1882, therefore becomes the proper designation of the species treated in my revision (loc. cit. p. 121) as *A. lanuginosa* HBK. Nov. Gen. 3:193. 1819, non Nutt. (1818). All references to *A. lanuginosa* HBK. should be changed to read *A. otarioides* Fourn.

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Annals
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AN ANALYSIS OF INTROGRESSION IN A POPULATION OF STEMLESS WHITE VIOLETS*

EDGAR ANDERSON

Speciation in the stemless white violets has generally been recognized as complicated. There are numerous taxa; variability from plant to plant in any one population is frequently high; and differences from one population to another are sometimes of uncertain interpretation. Careful field and herbarium work (Fernald, 1950, and Russell, 1953) has cleared up some of the complexities but considered in the large has raised as many problems as it has solved.

On two occasions I have had the opportunity to make brief but intensive studies of local populations, once in Minnesota with Dr. Norman Russell, once in Pelham, Massachusetts, with Dr. R. P. Levine and the biology majors from Amherst College. On the latter trip, two days were spent examining variable local populations of *Viola pallens* in the Pelham Hills. They were studied in the field; a critical mass collection was made; the variation patterns were analyzed in the laboratory, first morphologically, and then by simple statistical and semigraphical devices. From the data, introgression with a second taxon was established and a detailed technical description of it was drawn up by the method of extrapolated correlates. A second field trip confirmed the presence of just such a violet in the same area (the Pelham Hills), but since it was just barely coming into flower further studies of it were not possible. Neither species grows in the neighborhood of St. Louis, nor could readily be grown there because of climatic and soil differences. No further work with the problem is planned, but the data and the analyses are being put on record since they illustrate certain phenomena of introgressive variability which are of general importance. I am indebted to Dr. Levine for the opportunity of making this analysis and to a score of his colleagues and students for technical assistance.

After the mass collection was brought back to the laboratory, flowers from each plant were placed in numbered culture dishes to prevent withering, and special features of the variation pattern were assigned to groups of two to four students, first for morphological analysis and then for measurement. As soon as the measure-

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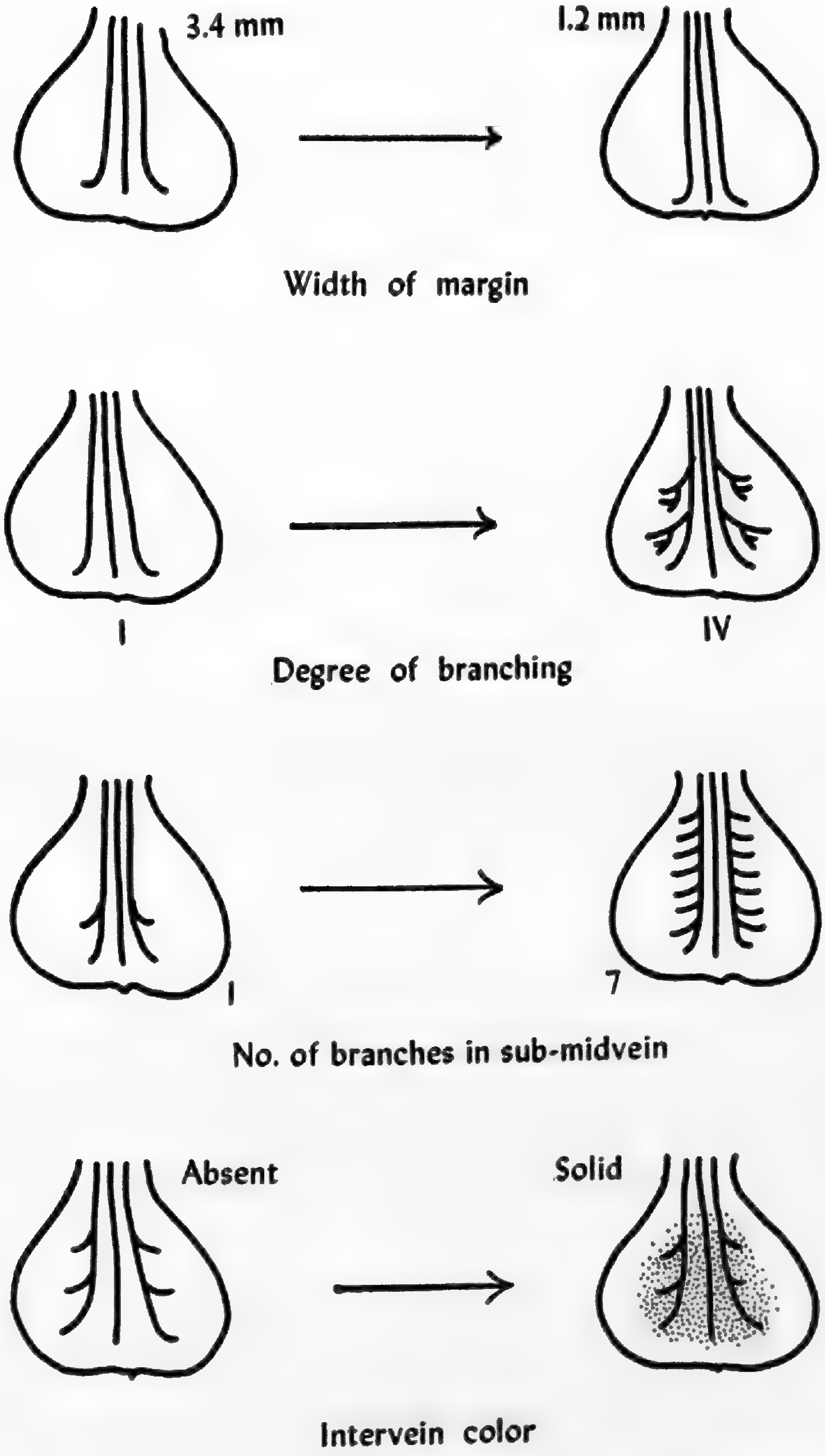
* A grant from the National Science Foundation made it possible to prepare for publication the four papers on Introgressive Hybridization published in this number of the ANNALS.

ments were completed, frequency distributions of each variable and scatter diagrams indicating the relationships between variables were prepared. One pair of students assisted in coordinating the work of the entire laboratory, seeing that each group studied each plant and that the measurements and grades were added to the master list. In this way the equivalent of several days of technical work was completed in one afternoon.

Vegetative propagation is well developed in *Viola pallens*. Nearly all the plants examined bore several flowers and a few of them made large mats with numerous blooms. This was taken advantage of in two ways: (1) Examination of the variation within and between plants made it possible to choose characters which were relatively independent of environmental effects. (2) In selecting flowers for measurement, great care was taken to choose a specimen which was typical of the plant on which it was borne. This minimized the effects of insect attack and other injuries.

It was soon apparent that the most conspicuous plant-to-plant variable in the population of *Viola pallens* was the amount of color on the lower petals. Repeated experience with such problems in various genera of plants and animals has demonstrated that by persistence and biological acumen a vague difference of this sort can nearly always be broken down into numerous more-primary variables each of which can then be dealt with quite precisely. Various means were tried out for recording and measuring the plant-to-plant differences in colored veins in terms of such primary features as number and position of veins, branching of veins, width of veins, deposition of color between the veins, and the like. In the time available it was possible to resolve the variation in color into the primary variables shown in fig. 1.

Other obvious variables in the population were leaf shape, leaf color, leaf pubescence, and the clubbed hairs towards the base of certain petals. It was not possible to find an effective way of measuring the latter variable. The hairs were varying in size, in the closeness of their spacing, and in the pattern of their distribution on the petals. In some flowers they tended to be in regular lines, in others not. Sometimes they were more dense in certain areas, sometimes not. There were obviously several different variables at work here, but in the time available it was not possible to pin them down. One of the basic difficulties was that *Viola pallens* is typically without any such hairs on the wing petals, and there is therefore no direct method by which we can determine its basic hair pattern (a very different thing from hair presence). This illustrates a major point to be kept in mind in the analysis of introgressive variability. Glabrous species, when hybridizing with pubescent species, nearly always bring in strong hair patterns of their own which of course are invisible in the species in which they originated. Similarly, white-flowered species when hybridizing with species whose flowers are colored nearly always bring in color modifiers and color patterns which were invisible or virtually so in the species whence they came. White-flowered species, for instance, are frequently genetically blue, though they may show no color or only a few lines or flushes of dark blue. If such a species is crossed to one with bright magenta-pink



Width of margin

Degree of branching

No. of branches in sub-midvein

Intervein color

Fig. 1. The four variables which were responsible for the variation in color in the spur petals. The extremes within the population are shown somewhat diagrammatically. The spur petals are shown as if they were always the same size and shape; actually they varied a great deal for these characters.

flowers, and this hybrid back-crossed to the white, the resulting three-quarter bloods will show blue or light blue in many of the flowers. This statement is based primarily upon genetic data from the breeding of Brachyceras water-lilies, from introgressive experimental evidence from *Oxytropus albiflora* and *O. Lambertii* (Anderson, 1953), from hybridization between *Aquilegia flabellata* and *A canadensis*, and from observations on wild and garden hybrids in the genus *Phlox*.

Leaf shape would have been easier to analyze had the leaves been fully mature. Color and pubescence could have been scored in the leaves but as a matter of convenience were scored in the peduncle of the flowers.

After these several variables had been analyzed and measured it was simple to demonstrate by means of a pictorialized scatter diagram that they were organized in two complexes. The more closely it was possible to follow all seven of them, the easier it was to demonstrate that these six *on the average* tended to associate themselves in the following combinations:

Wide margined petals	Narrow margined petals
Few colored veins	Many colored veins
Colored veins unbranched	Colored veins branched
No color between veins	Highly colored between veins
Glabrous pedicels	Pubescent pedicels
Little or no anthocyanin in epidermis of peduncle	Much anthocyanin in epidermis of peduncle

When the specimens had been graded in terms of all seven variables it was possible by comparing the two extreme classes (i.e., those which were low for all seven of these characters vs. those which were high for all seven) to add the following characters to these complexes:

Very early flowering	Later flowering
Delicate	Coarser throughout
Highly fragrant	Little or no fragrance

Extrapolating character by character we drew up the following technical description of the hypothetical species which could account (by hybridizing and back-crossing) for the variation pattern in this population:

A later-flowering, less fragrant, slightly coarser species than *V. pallens;* peduncles pubescent, strongly tinged with anthocyanin; flower white, the lower three petals conspicuously veined with purple and with a blue-purple blotch in the center of the keel petal; wing petals most probably with clubbed hairs near the base. Much of this description would apply equally well to either *Viola blanda* or *V. incognita,* two similar (and frequently confused) species of eastern North America. On the second field trip violets answering this description were found in close proximity to those previously collected. They were so much later in their flowering season that the details of their color pattern could not yet be precisely determined.

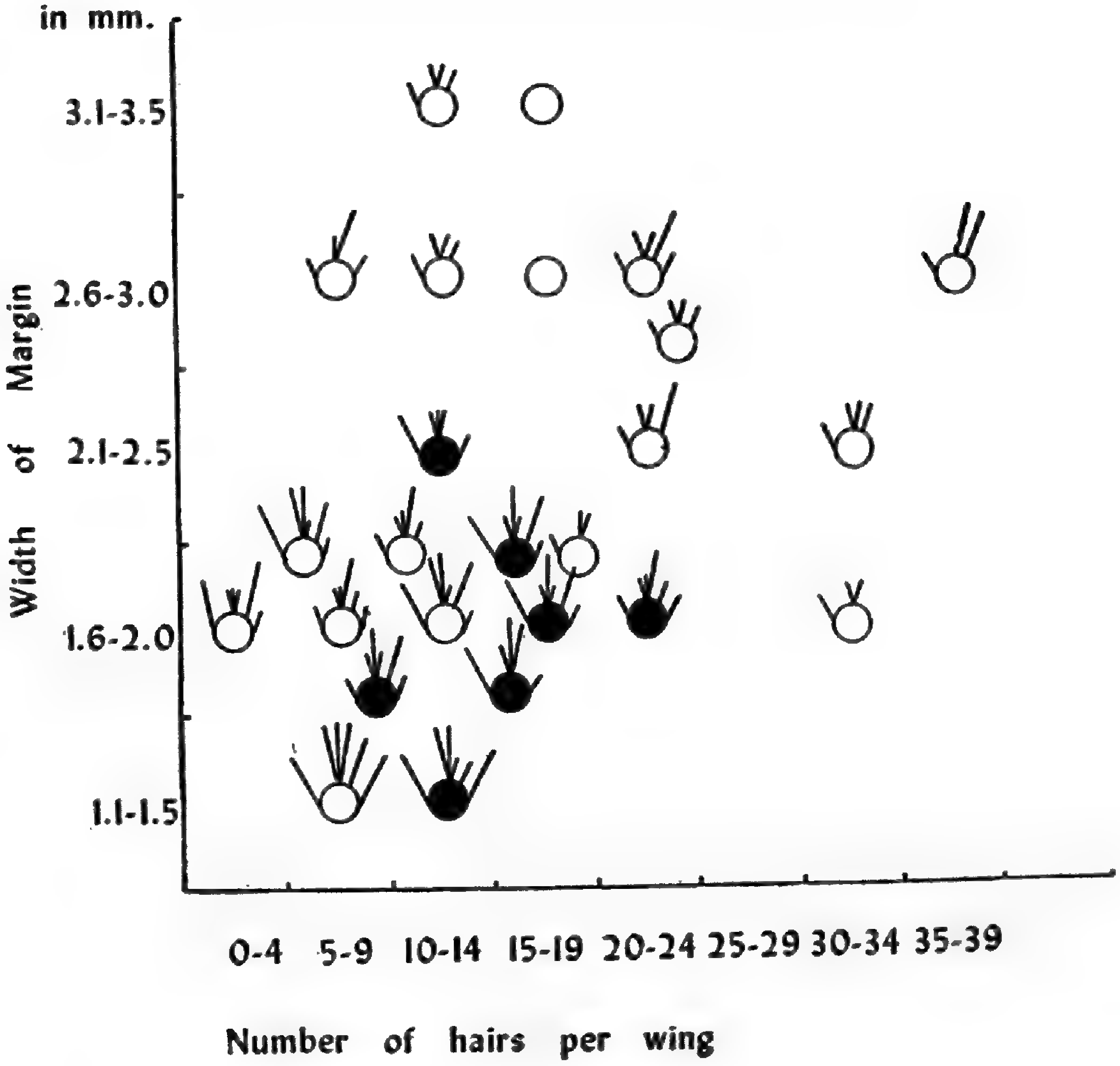


Fig. 2. Pictorialized scatter diagram showing the variation for seven characters in the population studies. Each circle represents a single individual. Black circles denote a flower with a heavy blotch on the spur petal.

Two of the characters are indicated along the margins. It will be noted that the number of hairs shows no very definite association with any of the other characters.

Five characters are indicated by rays:—

The rays departing from the equator of each dot designate the number of branches in the submedian veins: no equatorial ray, 1 branch; 1 short ray to the left, 2–3 branches; 2 short rays, 4 branches; 1 long and 1 short ray, 5 branches; 2 long rays, 6–7 branches.

Number of wing-petal veins shown by the apical ray which slants to the left: no ray, 0–3 veins; short ray, 4–7 veins; long ray, 8–10 veins.

Hairs on pedicel shown by erect apical ray: no ray, 1–4 hairs; short ray, 5–9 hairs; long ray, 10–13 hairs.

Degree of branching shown by apical ray slanting to the right: no ray, branching of first degree only; short ray, branching of second degree; long ray, branching of third or fourth degree.

Position of pedicel hairs shown by shoulder ray slanting to right (at the right between the apical and equatorial rays): no ray, no hairs or hairs very faint; short ray, hairs extending up to crook of pedicel; long ray, hairs extending fom part way up to the crook of the entire pedicel.

From the data presented here, the introgression responsible for the variation in this population of *V. pallens* might have come from either *V. blanda* or from *V. incognita.* The presence of clubbed hairs on the wing petals of many of the plants, as well as the general distribution patterns of both species, would indicate that *V. incognita* was certainly involved. The fact that clubbed hairs on the wing petals did not seem to be closely associated with either complex would suggest that both *V. blanda* and *V. incognita* might be involved, were it not for the difficulties in assaying hair pattern in glabrous species which have already been discussed. A field study similar to this one carried on a fortnight later in the spring in the same locality would probably yield critical evidence on these points.

After the differences between *V. pallens* and its introgressants had been analyzed it was easy to demonstrate the relationship between the micro-distribution of the introgressants and the ecology of the site. The road wound through a hilly region of second-growth forests which were beginning to resemble well-established mixed hardwoods with silver birch, hemlock, maple, and ash. The actual roadway and its drainage ditches had been repeatedly relocated, and extensive grading had been carried on within a few years. The plants of *V. pallens* in the woodlands showed a minimum of introgression whereas collections from the ridges of excavated soil along the roadside showed a maximum of branched veins, blotched petals, etc. This increased degree of introgression in disturbed sites has frequently been reported and its general significance made the subject of a special study (Anderson, 1948).

CONCLUSION

Increasing experience with species hybrids in the field and the experimental plot has shown that what looks like a simple difference between two species can often be broken down into a number of more primary ones, each of which is itself apparently multifactorial. In this example the difference between a heavily marked spur petal and a lightly marked one can be demonstrated as resulting from the following more basic differences:

Number of colored veins
Branching of veins
Restriction or non-restriction of colored veins to center of petal.
Interveinal blotching.

In *Adenostoma* (Anderson, 1952, 1954) dense versus open panicles can be demonstrated as resulting from the following more basic differences, each of which behaves as if it were multifactorial and is only loosely associated with any one of the others:

Long vs. short internodes
Non-telescoped vs. telescoped internodes
No evident tertiary branches vs. many evident tertiary branches
One flower per node vs. several flowers per node.

The field analysis of such examples of introgression as that just described should enable us eventually to find our way to the most efficient techniques and best experimental materials for detailed genetic analysis of quantitative characters. This entire field of Genetics, as a truly experimental science, has scarcely advanced in effective techniques since East first established the multiple-factor hypothesis and set up a series of criteria for testing it. Modern work on the subject has been largely confined to expertly contrived mathematical models, indicating how quantitative characters might evolve. While very stimulating, these models are a long way from any really concrete evidence showing chromosome by chromosome and segment by segment how any particular character is inherited or, on the other hand, demonstrating with incontrovertable proof how any particular chromosome is organized in between the marker genes.

This paper is one of a series illustrating exact techniques for the morphological analysis of variable populations. These techniques are at last approaching the precision which will permit their use in decisive experiments on the genetics of quantitative inheritance. These studies have seemed to most observers as a means by which the exact methods of Genetics could be used to illuminate the problems of Taxonomy. They are now beginning to be revealed as an attempt to refine from the wider observational basis of Taxonomy, precise evidence for analyzing a basic problem in Genetics. Logical deduction, no matter how acute, cannot serve forever in the place of direct evidence on so fundamental a question.

SUMMARY

Field studies of a population of *Viola pallens* resolved the bulk of the variability into two complexes, one of which is *V. pallens* and the other a later, slightly coarser, and more deeply pigmented species. The purple petal spot of this latter complex is shown to result from the following more primary variables, each of which is apparently multi-genic:

Wide marginal area without veins	Narrow marginal area
Few colored veins	Many colored veins
Few branched veins	Many branched veins
No interveinal color	Heavy interveinal color

The bearing of such studies on the genetics of quantitative inheritance is specifically pointed out.

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"SOME PECULIARITIES OF MAIZE IN ASIA" BY N. N. KULESHOV

Translated by HAROLD J. KIDD and HOWARD C. REYNOLDS

Illustrations re-drawn from the published photographs by Ellen Kern Lissant

TRANSLATORS' NOTE: The following is a translation from the Russian of a paper by N. N. Kuleshov (Bull. Appl. Bot., Genet., and Pl. Breed. 19:325–374. 1928. English summary, pp. 370–374). It is of particular interest in view of recent findings concerning the geography of races of maize. The only extensive studies of maize in the Orient are here described by the author. Kuleshov's entire work has been translated and included with the exception of his literature review of the American studies of waxy maize.

The English used in this translation will strike a number of people as being quite repetitive and wordy. For instance, the word *obraztsy,* which we have translated *collections,* appeared again and again. This characteristic, along with the redundant phrases and wordiness, has been retained wherever the meaning was sufficiently clear. We have attempted to retain in English something of the quality of the Russian original.

Regarding the references missing from the *Literature Cited,* we should mention in fairness to Dr. Kuleshov that there are innumerable evidences of careless editing.

In the work of the American investigators, G. N. Collins and J. H. Kempton, one meets an array of very interesting characters and attributes which are unknown in maize from the American continent but which were discovered in collections of maize from Asia.

During the years 1926 and 1927, relatively vast amounts of material [data] concerning the maize of Asia passed through the All-Union Institute of Applied Botany, being composed of both laboratory and field studies. From this material it was possible to expand the observations of Collins and Kempton and to establish an array of new peculiarities in the maizes of Asia which are unknown to the American investigators.

Since we are planning a future publication of the complete work on Asian maize, in the present preliminary communication we will briefly bring out only the most interesting of the facts which have been established.

All the material which has been studied up to the present time is listed in the following table, and consists of collections from different regions of Asia and Transcaucasia:

1.	Asia Minor	65 collections
2.	Persia	10 collections
3.	Afghanistan	24 collections
4.	Turkestan	65 collections
5.	The Primorskiĭ [Maritime] Province	85 collections
6.	Manchuria	51 collections
7.	Western China	18 collections
8.	Japan	5 collections
9.	India, Ceylon, Java	6 collections
10.	Armenia	59 collections
11.	Azerbaijan	10 collections

We will first pause to refer to the American work, passing thereafter to the data of our investigations.

I. THE DATA OF THE AMERICANS' CONCERNING THE MAIZE OF ASIA

[Omitted]

II. OUR OWN INVESTIGATIONS ON THE MAIZE OF ASIA

1. WAXY MAIZE

In the collection of maize which is located at the All-Union Institute of Applied Botany and New Crops, the presence of the type *waxy* was established in several cases.

(1) Of two collections received from the expedition of V. V. Markovich to Shanghai, one collection (on the cob) was white with a single blue kernel. The other (shelled corn) was called "Buo Rew" and contained a mixture of flinty, tooth-like yellow kernels along with an admixture of a single grain of the waxy type which had a light yellow color. Both collections were received in 1927.

(2) Four collections were received by the Institute from the experiment Station "Eho" in northern Manchuria, and in all four the waxy kernels have a yellow color of varying intensity. For two collections, the source was not designated, but for two it is known: Maize no. 136 "Nyan-pao-mi" ("sticky") from Ninguta, and maize no. 137 "Nyan-pao-mi" from Tubin. Both of these localities are in northern Manchuria.

(3) Two collections were received from the Primorskiĭ Experiment Station. Their source was the village of Lukyanovka in the Utkin district, the Spassk territory of the Primorskiĭ [Maritime] Province. One collection, no. 59, consists only of waxy maize of a light yellow color, which indicates that this sort has been cultivated here for more than twenty years. The second collection, no. 57, is principally flinty, but as an admixture it has a single kernel of the waxy type.

A comparison of all the collections listed above with the original collection received from Collins confirmed their undoubted classification as the waxy type.

We pause to consider the meaning of these findings. The collections from the region of Shanghai, received from V. V. Markovich, confirm once more the fact, which is known from the American literature, that waxy maize was discovered

Fig. 1. Plant of waxy maize, from Collins (1909).

and cultivated in this region. The collections from Ninguta and Tubin, which were sent by the Eho Station, establish a new place of discovery of waxy maize, which is significantly different from those three regions (Shanghai, Burma, and the Philippines) in which this maize was previously known.

In the seed catalogue of the Eho Experiment Station, these collections are filed under the name "Flint Corn, that is, flinty maize", but are labelled with the Russian name "Kleikaya" (sticky), and also the Chinese name "Nien-pao-mih". This Chinese name is differentiated from the other Chinese names "Pai-pao-mih", "Hei-pao-mih", and "Huang-pao-mih". There are, in the catalogue of the Eho Station, other cultures of flinty maize which force the supposition that the local populace differentiates this sort of maize from the ordinary flinty maize[1]

The collections from the village of Lukyanovka, which is located approximately 300 kilometers east of Ninguta in the direction of Vladivostok, may be assumed to have a common origin with the waxy maize which is cultivated in Ninguta. None-the-less, on the basis of their being found here, we have sufficient grounds to assume that the growing of maize of the waxy type in this northern region of eastern Asia is wide-spread and is not especially rare.

If we now compare our apparently new discovery of waxy maize with what was previously known concerning its cultivation, we obtain the following: the Philippine Islands[2] are located at 5–15° north latitude; the upper Burma regions, 23–26° n. lat.; the Shanghai region, 31–32° n. lat.; the village of Lukyanovka, 43° n. lat.; Ninguta, 45° n. lat. Thus, at the present time, the area of diffusion of waxy maize has extended great distances from north to south, having been discovered in 1908 at Shanghai, again in 1915 in upper Burma, and 1920 in the Philippines. With our discovery [known] waxy maize immediately moves far to the north. This finding permits us to hypothesize about the limits of diffusion of this type in eastern Asia, but the incompleteness of maize investigations in this territory does not permit us to speak with certainty.

The matter of the extent of the limits of cultivation of waxy maize westward is of great interest. We have, unfortunately, insufficient material with which to trace the spread completely and clearly. At any rate, our material permits us to say with certainty that there is no waxy maize in central Asia or in Asia Minor. Turkestan was covered by us completely and in detail, from the China border to the Caspian Sea. Afghanistan was thoroughly explored by N. I. Vavilov, while P. M. Zhuzovskiĭ travelled for two years in Asia Minor, and in neither place was waxy maize discovered. In 1927 we received eighteen collections of maize which were collected in western China from our consul in Kashgar, in none of which was there waxy maize. We have not yet spoken of the collections from the Caucasus and European areas. Here, of course, *waxy* does not occur.

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[1] The list of available seed at the Eho Station for exchange with other experiment stations. K. V. Zh. D., Harbin, 1926.

[2] These localities are those mentioned in the omitted review of American literature.

Fig. 2. Typical brachytic maize (from Kempton, 1921).

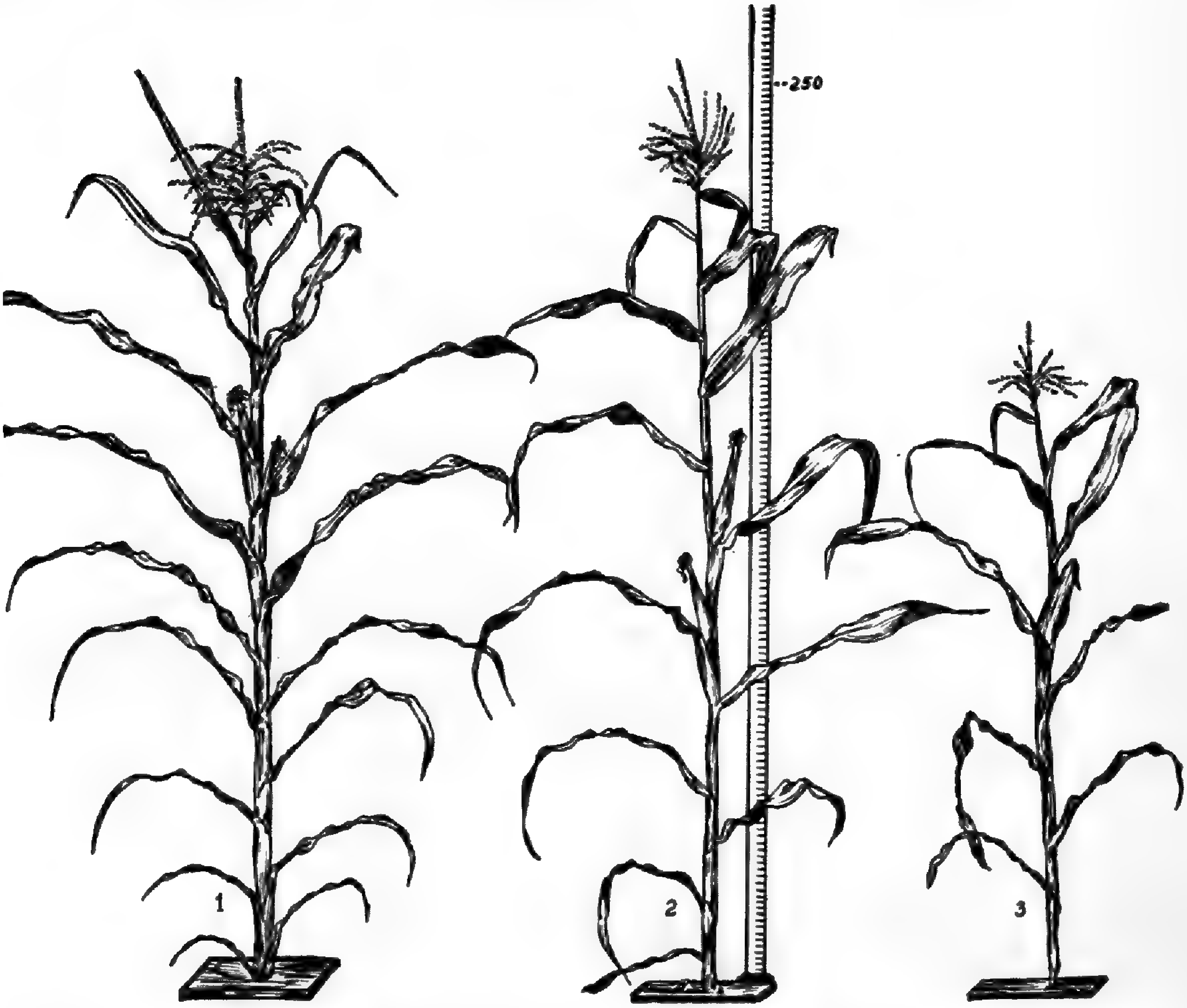

Fig. 3. The most widespread types of maize plants from Manchuria and western China, grown in Kharkov, 1927. Plants like Nos. 2 and 3 are more frequent in Manchuria.

In 1926 and 1927 we were fortunate enough to receive exceptionally interesting material from America. The expedition of S. M. Bukasov, of U. N. Voronov, and of S. V. Usepchuk brought us specimens of maize from Mexico, Guatemala, Panama, the island of Cuba, Venezuela, Colombia, Peru, and Bolivia. Approximately 2,000 collections were sent in all, representing a remarkably unusual variety of types. And here, in the principal center of variation from which maize originated, we, repeating the experiment of Collins,[3] did not find maize of the type *waxy*. Thus, this particular type of maize is, apparently, peculiar to eastern Asia.

Since we already had in our collections samples of waxy maize, we planted them in 1927 and observed differences in their vegetative character. The majority of plants in collections from Shanghai had the attributes which were described by Collins: stiff leaf blades, silking ears hidden by the leaf sheaths, and the upper leaves displaced to one side and covering the panicle. The collections from Ninguta and Tubin were very singular in aspect, being thin-stalked plants with absolutely no tendency to produce lateral shoots. It is possible, however, that the conditions

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[3] Apparently the testing of kernels for the presence of waxy endosperm.

in Kharkov in 1927 contributed greatly to this situation, causing a small number of leaves and well-exserted panicles to be produced. This aspect was not peculiar to these collections only; similar plants predominated in all of the numerous Manchurian collections of flinty maize. Figure 3 depicts plants which are characteristic of the collections from Manchuria. For the most part, one encounters plants II and III, plant I being particularly rare.

A collection of waxy maize from the Primorskiĭ Province was very extraordinary in its vegetative appearance and the make-up of its plants. All individuals were predominantly of the Manchurian type but among them were many plants similar to those we have termed the "European type". The latter is distinguished by stalks of average vigor which produce one to two lateral stalks similar in degree of development to their main stalk under favorable conditions, as is characteristic of the European flints. In individual plants one could observe attributes described by Collins for Shanghai maize: assymetrical upper leaves which are straight and which cover the silking ears in their axils at the time pollen is shed (fig. 4).

TABLE II*

PHENOLOGICAL OBSERVATIONS ON SAMPLES OF WAXY MAIZE

	Date seeded	Date of shoot emergence	Date of pollination	Date of silking	Date of ripening	Plant height	Number of leaves
Shanghai from Markovich	5/12	5/28	8/25	8/27	....	....	20.7
Ninguta	5/12	5/28	7/23	7/22	9/12	207	17
Primorskiĭ Province	5/12	5/28	7/19	7/23	9/12	188	17

* Table I is not included, since it was reprinted from Kempton (1921) in the omitted part of this paper and was not referred to elsewhere.

The data from phenological observations and measurements are presented in table II, representing individuals of the waxy type cultivated by us in Kharkov. Unfortunately, we were unable to compare them with Collins' plants from Shanghai, due to the fact that the seed of the latter had become inviable since its receipt at the Institute in 1923. The data in this table demonstrate that the Shanghai collections of V. V. Markovich were very late under Kharkov conditions, commencing flowering on August 25, and failing to ripen before the first killing frost on October 15. The collections from Ninguta and the Primorskiĭ Province were very similar to one another and should be classed as early in maturity. The Shanghai collection is distinguished also from the other two by its large number of leaves.

In the collections from Ninguta it is interesting to note that the silks appear before pollen is shed. The plant height of the collection from Ninguta also indicates its dwarfness.

Fig. 4. Diversity of plants of waxy maize from the Primorskiĭ Province, grown in Kharkov, 1927.

The above remarks on the vegetative peculiarities of our collections of waxy maize indicate that only the Shanghai collection was similar to that described by Collins in his first paper (1909). The Primorskiĭ collection was similar in vegetative characters to the collections of flinty maize of that region. The Primorskiĭ collection reflects the influence of the Manchurian type, on one hand, and the European, on the other. The latter has a wide distribution in the Primorskiĭ Province, to which it had been brought by the Ukrainian settlers. A mere trace of the Shanghai type is retained by these plants. This fact is merely given and causes no surprise, since from the work of Collins we know that the endosperm factor *waxy* in his investigations was not linked with the vegetative attributes of the plant. However, such being the case, that in northern Manchuria waxy maize steadily acquires the aspect peculiar to most of the maize in this region, this observation attests to the fact that here waxy maize is not a newcomer.

Due to a misunderstanding, waxy maize has not yet received a generally accepted scientific Latin name, and different authors vary in referring to it. Americans usually use the term *waxy* but sometimes use the term *Chinese,* while German authors use *wachsig* or *chinesische,* etc. Since waxy maize of the average group as distinguished by Sturtevant occupies a special place, we suggest the Latin name *Zea mays ceratina* Kuleshov (spec. nov.).

2. THE PERSIAN TYPE OF MAIZE

In 1926, a large number of collections of maize were brought to two points, Kharkov and Sukhum. Almost the entire world was represented and the number of collections which were planted at both these two points approached 1,500. On the basis of the enormous amount of vegetative diversity in the collection, the Persian plants were sharply differentiated by their short height and the general condensation of the plant structures, as were those collections from the regions of middle Asia and Transcaucasia which border Persia.

These collections were again grown in 1927, and the peculiarity of the above specimens was again sharply distinguished from the variety of the world-wide collection, in spite of the exceptionally favorable conditions during the growing season. The 1927 study of these collections demonstrates that, besides shortness, the plants possessed an array of other extremely interesting peculiarities. The peculiarity [probably shortness] was expressed by all collections from Persia which were studied, so we therefore termed this completely different appearance of maize plant the Persian type.

Let us now turn our attention to the characteristics of the collections in which the manifestations of the Persian type may be observed. Persia was represented in our seedlings by seven collections from Seistan and Zurabad, all of which were distinguished by the following characters: (1) shortness of the plants; (2) coarse, wide, and short leaves with stiff blades; (3) definite waviness of the leaf blades; (4) the poor exsertion of the panicle which is covered by the stiff upper leaves; (5) the non-emergence of the silking ears at tasseling; (6) the correlation of the blooming of the male and female inflorescences, frequently developing protogyny. Figure 5 shows many of these characters very well. One may observe the shortness of the plants, the stiffness of the leaf blades and the waviness of their surfaces, the manner in which the stiff upper leaves cover the panicle, and the nearly-hidden silks of the plants in the leaf axils, illustrated under a higher magnification in fig. 6.

While closely related in the majority of these characters, several Persian collections were distinguished by their capacity to produce lateral shoots. Of seven collections grown in the field, five were characterized by an almost complete lack of the capacity to produce lateral shoots both years, whereas two collections expressed this capacity rather strongly. We must needs note, however, that the plants at the edges of the plots were observed to be surprisingly uniform in appearance. Figure 7 shows the vegetative appearance of the plants of the collections from Persia. The plant on the extreme right represents the striking bushiness of the Persian type plants.

The above photographs [illustrations] doubtless have shown the peculiarities of the plants which we have distinguished as the Persian type. However, for a more complete picture, we present several measurements of plants of the Persian type for comparison with measurements of the prevailing sorts, Minnesota 13 *(indentata)*, and Longfellow *(indurata)*, as well as the original *brachytic*, which was received by us through N. I. Vavilov from Emerson of North America. As

Fig. 5. Typical plant of Persian maize, grown in Sukhum, 1927.

indicated, the growing conditions during the seasons of 1926 and 1927 were very different, 1927 being much more favorable and producing more vigorous development of the plants. But since Minnesota 13 and Longfellow were sown both years, an opportunity for a comparison [of the plants in both seasons] still remains. *Brachytic* was sown only in 1927.

TABLE III

OBSERVATIONS ON MAIZE PLANTS IN 1926 AND 1927 (KHARKOV)

Name	Origin	Plant height		Number of leaves on main stem		Stem thickness		Number of stems		Panicle exsertion		Number ears per plant	
		'26	'27	'26	'27	'26	'27	'26	'27	'26	'27	'26	'27
Persian 1701	Zurabad	94	104	......	16.3	......	1.5	1.0	1.0	0.4	2.0	1.0	2.0
Persian 1702	Zurabad	92	116	17.2	17.4	......	1.7	1.1	1.2	0.3	1.2	1.6	3.1
Persian 1698	Seistan	96	142	18.8	18.5	......	....	1.6	2.3	0.6	3.0	2.9	6.3
Brachytic	Emerson	......	118	......	24.0	......	2.4	....	1.0	....	1.0	....	1.0
Minne. 13	U. S.	147	211	15.4	16.0	......	1.7	1.0	1.4	5.8	7.5	1.0	1.4
Longfellow	U. S.	140	229	14.8	16.5	......	2.2	3.6	4.4	....	6.7	1.1	1.6

Let us view the data from the table (Table III). The shortness of the Persian type plants, in comparison with the other collections, is shown perfectly clearly. Collection no. 1701 was half as tall in 1927 as Minnesota 13 or Longfellow. It was even shorter than *brachytic*, having a height of 103 cm. as compared with 118 cm. for *brachytic*. In the number of leaves, the Persian collections exceeded Minnesota 13 and Longfellow, but were surpassed by *brachytic*, which produced 24 leaves.

As indicated above, a terminal brachyism produces a reduction of plant height by means of a shortening of the internodes, without reducing the number and length of other parts of the plants. It is interesting, in this connection, to compare the average length of internodes of the plants studied by us. Table IV presents the results of the appropriate computations on the data from Kharkov. The figures from this table tell us that the mean internode length in the Persian collections of maize show significant reduction in comparison with the common types. They do not approach the shortness observed in *brachytic* but in any case a deviation from the norm is indicated.

The thickness of the stems of the Persian collections is not only no less, but even somewhat greater than the taller farmer's varieties. All of these characters (shortness of plant, a large number of leaves, and thick stems), considered together, give the impression of a condensation of plant structure, approaching the appearance of *brachytic* in several respects.

TABLE IV

MEAN LENGTH OF INTERNODES IN MAIZE PLANTS, IN CENTIMETERS

	1926	1927
Persian 1701	....	6.16
Persian 1702	5.35	6.55
Persian 1698	5.11	7.68
Brachytic	....	4.92
Minnesota 13	9.55	13.2
Longfellow	9.46	13.8

The exsertion of the panicle is perfectly clear from the figures in Table III. At the time during which the distance from the highest leaf to the lower panicle branches was calculated, in Minnesota 13 and Longfellow it was 6–7 cm.; in the Persian collections in 1927, it was 1–3 cm., but in 1926 it did not approach 1 cm., in several instances being even less than zero, that is, the panicle had not completely emerged from the sheath of the upper leaf. In *brachytic* the exsertion of the panicle in 1927 was 1 cm.

Due to the small number of stems, the Persian collections nos. 1701 and 1702 present a characteristically non-bushy aspect, whereas no. 1698 is typified by a significant bushiness. The number of ears per plant of Persian maize is greater than in the types in common culture. In 1927 collection no. 1698 produced an average of 6.3 ears per plant.

Let us continue with a brief glance at the data of the phenological observations (Table V). In the length of the vegetative period the Persian collections present several types earlier than the farmers' varieties. But the essential peculiarity of their differentiation does not lie here. They are distinguished from the common types by their peculiar nature of flowering. As demonstrated in one of our previous

TABLE V

PHENOLOGICAL OBSERVATIONS IN 1927 AT KHARKOV

Collection	Date of seedling emergence	Date of pollination		Silking date		Ripening date
		10%	75%	10%	75%	
Persian 1701	5/27	7/27	8/3	7/25	8/2	9/20
Persian 1702	5/27	7/27	7/31	7/22	7/29	9/20
Persian 1698	5/27	7/27	7/31	7/23	7/31	9/20
Minne. 13	5/26	7/14	7/19	7/14	7/23	9/28
Longfellow	5/31	7/21	7/27	7/23	7/30	9/28

Fig. 6. Concealment of the silk in the axil and sheaf of the leaf in Persian maize, grown in Kharkov, 1927.

works, "the appearance of the silks lags approximately three days behind the shedding of pollen under conditions at Kharkov" (Kuleshova and Kuleshov, 1918). In contrast to what was published by us earlier as the usual order of flowering of maize under Kharkov conditions and to the observations on Minnesota 13 and Longfellow in 1927, the Persian collections began extruding silks several days earlier (2–5) than the onset of pollination, giving an especially clear protogynous character to the flowering instead of the protandry which is common for maize. This phenomenon must be met with very rarely in maize. In one of his papers Collins states that until 1912 he had not encountered a protogynous race of maize, and in 1912 practically all plants from two ears of "red pop corn" from Spain were protogynous (Collins, 1913). He also believes that the presence of a receptive stigma earlier than the onset of pollination aids self-pollination. We see a confirmation of that in the frequently striking uniformity of the plants of the Persian type, which remind one of the uniformity observed in "selfed strains".

Turkestan collections in the field present a fairly large diversity in vegetative type, but the average of this diversity is an array of collections which repeats the general picture of vegetative appearance which is given by the Persian collections. In fig. 8, the principal representative of the vegetatively diverse Turkestan maize is depicted. In nos. 4 and 5 we recognize the characteristic plants of the Persian type in the form of two of its variants—tillering and non-tillering.

Fig. 7. Vegetative diversity of maize plants in Persian collections grown in Kharkov, 1927. Collections Nos. 1701, 1702, and 1698 (from left to right) from Zurabad and Seistan.

The Persian type of plant was established for the following collections:

1. Collection no. 1449 from Mary (Merv).
2. Collections nos. 3434, 3435, 3436, 3437, and 3439 from the Shirabad region.
3. Collections nos. 3450, 3451, 3452, 3453, 3454, and 3455 from the Polotansk region.
4. Collection no. 3425 from Termez.
5. Collection no. 2783 from the Zerevshansk region.
6. Collections nos. 3388, 3389, 3390, 3391 from the Urta-Zerevshansk district.

Nos. 1449 and 3425 share the characteristics of representatives of the Persian type. In Table VI we present several data characterizing these collections. In general, the data from the table are nearly like those which we presented for the Persian collections, which are distinguished by an increased number of leaves and by a shorter vegetative period. These collections do not silk earlier than pollination, but, in some instances, the flowering of the male and female flowers was more closely correlated in 1927 than it was in the common types. An apparent expression of the Persian type was observed in numerous collections from upper Turkestan. Besides the above, we observed different features of the Persian type in a host of collections from the Tashkent region, being expressed now in the stiffness of the leaves, now in the exsertion of the panicles, etc.

TABLE VI

OBSERVATIONS ON TURKESTAN COLLECTIONS IN 1926 AND 1927 AT KHARKOV

		1449 from Merv		3425 from Termez	
		1926	1927	1926	1927
Plant height		88	147	....	134
Number of leaves		21.0	20.1	....	19.5
Stem thickness		....	2.1	....	2.0
Panicle exsertion		0.0	2.8	....	2.3*
Number of stems		3.3	3.3	....	1.2
Number of ears per plant		1.4	5.1	....	2.2
Date of seedling emergence		5/25	5/27	....	....
Date of pollination	10%	7/30	8/6	....	8/4
	75%	8/8	8/12	....	8/9
Silking date	10%	8/3	8/5	....	8/5
	75%	8/13	8/10	....	8/9
Ripening date		........**	10/2	....	10/2

* [Assumed. Original printing was "23".]

** Failed to ripen before frost.

Fig. 8. Vegetative diversity of maize plants in collections from Turkestan grown in Kharkov, 1927. Plants 4 and 5 are from collections 1449 and 3425 from Merv and Termez [respectively].

Fig. 9. Vegetative diversity of maize plants in collections from Armenia grown in Kharkov, 1927. Plant 4 is from collection 1632 from the Echmiadzin District.

In Armenia we also encountered a fairly large amount of vegetative diversity among the collections, the types of which are depicted in fig. 9. Plant no. 3 is distinguished among these plants by its short stature. In its basic features this plant is the same as the "bushy" Persian type, but with several deviations from the typical Persian plants. In the shorter plants of Armenia we observed only free-tillering types. Furthermore, their leaves were usually wider and longer than in the Persian type. In several collections they were significantly longer and had lost their stiffness. In Table VII we present data which are characteristic of the typical short plants from the Echmiadzin region in Armenia.

TABLE VII

OBSERVATIONS ON THE PLANTS IN COLLECTION 1632 FROM ARMENIA GROWN AT KHARKOV

Year	Plant height	Number of leaves	Stem thickness	Number of stems	Panicle exsertion	Ears per plant	Date of seedling emergence	Date of pollination		Silking date		Date ripe
								10%	75%	10%	75%	
1926	82	17.7	....	3.3	0.0	1.36	5/25	7/30	8/8	8/3	8/13	......*
1927	139	17.2	1.8	3.2	3.9	3.6	6/3	8/2	8/9	8/4	8/12	9/28

* Failed to ripen before frost.

Short plants which were almost exactly as described above were encountered in the following regions:

1. Collections 1625, 1636, and 1649 from the Erivan district.
2. Collections 1619, 1632, 1644, 1647, 1622, 1624, 1638, 1612, and 1705 from the Echmiadzin district.
3. Collections 1616 and 1709 from the Daralagez district.

Besides the collections which are enumerated above, we observed various indications of the Persian influence on collections which were derived from other regions.

TABLE VIII

OBSERVATIONS ON THE PLANTS OF SHORT HABIT FROM AZERBAIJAN, GROWN AT KHARKOV, 1927

Collection	Plant height	Number of leaves	Stem thickness	Number of stems	Panicle exsertion	Ears per plant	Seedling emergence	Date of pollination		Silking date		Ripening date
								10%	75%	10%	75%	
Apsheron 1782	140	20.1	2.7	1.0	2.3	1.5	5/29	7/24	7/31	7/24	7/31	9/20
Nakhichevan 1783	133	16.0	1.2	5.4	----	6.9	5/29	7/31	8/11*	8/2	8/13	10/2

* [Assumed. Originally printed "7/11".]

Fig. 10. Vegetative diversity of maize plants in collections from Azerbaijan, grown in Kharkov, 1927. Plants 4 and 5 are from collections 1783 and 1782 from Nakhichevan Rep. and the Apsheron Peninsula.

In Azerbaijan the presence of the non-tillering Persian type was established in collections from the Apsheron Peninsula. In the Nakhichevan region, which borders on Armenia, the variations of the Persian type as described for upper Armenia were seen (fig. 10).

Upon viewing the photograph more attentively, the zig-zag arrangement of the internodes of the plant on the extreme right may be observed. An instance of a similar zig-zag character was observed by Kempton in his studies of *brachytic,* which at once leads to a conjecture of a relationship between our short-stemmed and the well-known brachytic types. Data concerning the characteristics of the short plants which are represented in the photograph are given in Table VIII.

From the data presented, the aspect of the plants from Azerbaijan in comparison with what was stated concerning other regions is sufficiently clear. We wish to mention, however, that in the Apsheron collections we observed a remarkable correlation in male and female flowering time. The studies of the peculiarities of the maize plant which were investigated for the present paper and described under the name of the Persian type give a series of very interesting conclusions:

1. Maize plants short in height considering their normal number of leaves are represented in very widespread regions in central Asia and Transcaucasia.

2. The stiffness of the leaf blades also indicates that the Persian type is very widespread in these regions.

3. The degree to which the upper leaves cover the panicle is quite variable in its expression, indicating a rapid diffusion of the Persian type in the regions of central Asia and Transcaucasia as well as in eastern Asia. Fig. 11 represents the different types of this covering observed in Kharkov in 1927.

4. The concealment of the silking ears is no less widespread in these regions than the characters mentioned above.

We know (through an acquaintance with the work of the American workers) that Collins observed in collections of waxy maize from Shanghai: stiffness of the leaf blades, the panicle covered by the upper leaves, and the concealment of the silking ears. Our data demonstrate a wide distribution of these characters in Asia, as well as their correlation with a definite area. True, in our short plants of the Persian type we do not have that strong expression of brachyism observed by Kempton, but at any rate this shortness compared with normal plants or even with those having a somewhat greater number of leaves gives a basis for comparison with the expression of that character.

The study of the world-wide collection of maize which was conducted in 1926 and 1927 demonstrated that such precise expression of all the recapitulated characters and their delimitation to definite regions will not be observed anywhere else on earth: these extraordinary peculiarities are inherent only to the maize of Asia. The protogynous character of flowering, which is developed so clearly in the Persian collections of maize, is not so widespread in other regions of middle Asia and Transcaucasia. But, at any rate, the remarkable correlation of the timing of male and female flowering can be one of the very characteristic attributes of maize plants in central Asia.

We should still consider one morphological attribute which is frequently encountered in the maize of central Asia and Transcaucasia. This character is the shortening of the stem internodes. There are many exceptions among the described collections and the character may be met with in collections from different regions, but in central Asia it is more often seen than not. In conclusion, after all that has been related concerning the Persian type of maize, we think it necessary to give several geographical and agricultural interpretations of the observed facts. A study of the map [not in the original] of the geographical distribution of the described type of condensed, short plants will show that it is adapted to the driest regions, where agriculture is possible only under irrigation. It is also clear that this type of plant is adapted to the agricultural plains and lowlands. The expedition of the author in 1925, 1926, and in 1927, into Turkestan and Azerbaijan, and the expedition of E. A. Stoletova in 1925 and 1926 into Armenia completely and definitely attest to this fact.

In those regions in which the presence of the Persian type of maize was established, the maize fields are usually of very small area, since these regions are known to be essentially limited to the culture of cotton. Maize is here grown on the edges of cotton fields or as a kitchen-garden crop. The biological and agricultural description of the plant and the extraordinary adaptation of this crop plant to the diverse conditions of the region of its cultivation were of great interest. Its shortness and its condensed structure are very valuable characters for regions of irrigation, giving a plant steadiness against the wind and protecting it from lodging on softened irrigated soil (see Kempton, 1921). The nearness of the leaves to each other, as effected by the shortness of the stem internodes, causes them to shade one another, by which, apparently, a reduction of transpiration is obtained. The stiffness of the leaf blades, oriented parallel to the sun's rays and not perpendicular to them, represents a broad adaptation in the plant kingdom without excessive insulation of the leaf in hot dry areas. The rough cutinized leaf which, unfortunately, was not studied anatomically, may also be considered an adaptation for reducing transpiration.

In 1927 during the journey to the Iolotansk Experiment Station in Turkmenistan, which is located on the edge of the burning waterless desert of Karakum, we chanced to see burned areas on the leaves of the American variety of maize in the variety observation plots. The burning was caused by the hot dry winds "garmsil", which are peculiar to the central Asian regions. In the local collections there were no similar burns. The panicles are covered by the stiff upper leaves and the silking ears are hidden in the axils and sheaths of the leaves. Thus these delicate flowering organs are protected from the destructive action of the dry burning winds of the Asian desert.

The simultaneous appearance of the male and female flowers, facilitating the timely utilization of the pollen, must be recognized as very expedient under the conditions of central Asia, for in the dry hot air the flowers and pollen of maize cannot be abundant, nor can the germinating pollen grains.

According to their reports, the American investigators consider the character *brachytic* to be very important, especially for dry regions, and are working towards a combination of the productiveness of normal types of maize with the shortness

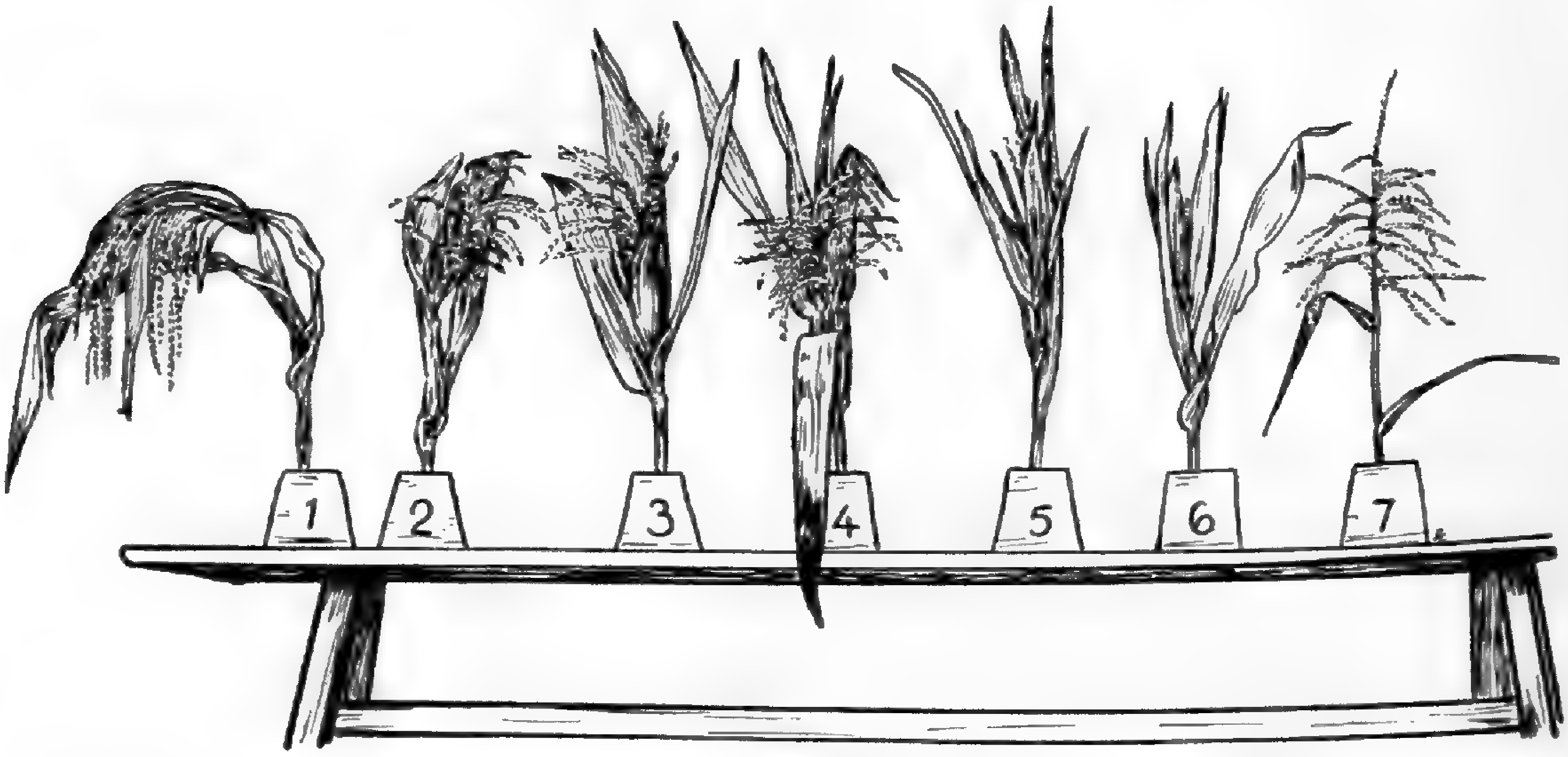

Fig. 11. Different types of covering of the panicle by the upper leaves. Plants 1 and 2, Primorskii Province; 3–6, Persia and Turkestan; 7, common open panicle. Kharkov, 1927.

of *brachytic*. In the collections described as the Persian type we have an undoubted approach to the resolution of this problem in that we have an entire array of other characters for the final stages of the important selection work to find a drought-resistant type of maize.

3. CONVERGENCE IN THE VEGETATIVE APPEARANCE OF THE PLANTS OF MAIZE AND SORGO ORIGINATING FROM THE SAME REGIONS OF ASIA

A great variety of crops which originated from widely different parts of the world were planted in 1927 at the Ukrainian Station of the Institute near Kharkov. These plants demonstrated that the place of geographical origin of many crops is mirrored in the array of general vegetative characters, notwithstanding the fact that they are classified in widely differing species, genera, and families. For example, the lucernes, flaxes, and wheats of north Africa are distinguished by a very intensive growth and differentiation in the early stages following germination. Flax, peas, and wheats from central Asia have a definite tendency toward dwarfness and slow growth in a number of collections. The lucerne of Turkestan has, in comparison with the lucernes of other regions, short internodes, slow growth, etc. Apparently, the ecological conditions which have been imposed on these crops in the current century have influenced them to the production of a general ecotype, the one most successfully responding to the conditions of the region.

While we were conducting a detailed study of a large collection of maize and sorgo in 1927 at the Ukrainian station of the Institute, in cooperation with V. I. Savron and A. I. Ivanov, we noted that a striking analogy was manifest in the aspect of the plants of maize and sorgo from the same regions of Asia. In the preceding section we described in detail, under the name *the Persian type,* a special type of maize which was distinguished by shortness in height and internodes. Maize, which is a new plant on the Asian continent, changed its aspect in central Asia in the very same direction as the oldest crops—flax, lucerne, etc. In the sorgo stocks A. I. Ivanov noted plants among the Turkestan collections which were distinguished by the very same short stems and broad leaves as were previously described for maize of the Persian type (fig. 12).

During our expedition to Turkestan in 1927, in cooperation with I. V. Gduzenko, we observed a striking resemblance in vegetative aspect between the plants of maize and sorghum in the field. In this respect the Geoktepe region of Turkmenistan is especially interesting. The very same short height was seen in sorghum in fields of the Shirabude Experiment Station near Bokhara. This dwarf sorghum is considerably less widely distributed in Turkestan than the common tall type, but we discovered it, nevertheless, in many places, in many regions (Geoktepe, Archman, Termez, Merv, etc.). In these same regions and places we almost always discovered the dwarf, condensed Persian type of maize plants.

In other regions of Asia—Manchuria, northern China, and the Primorskiĭ Province—there was also a striking resemblance in vegetative aspect between maize and sorgo which originated from the same region. Plots of maize and sorgo are

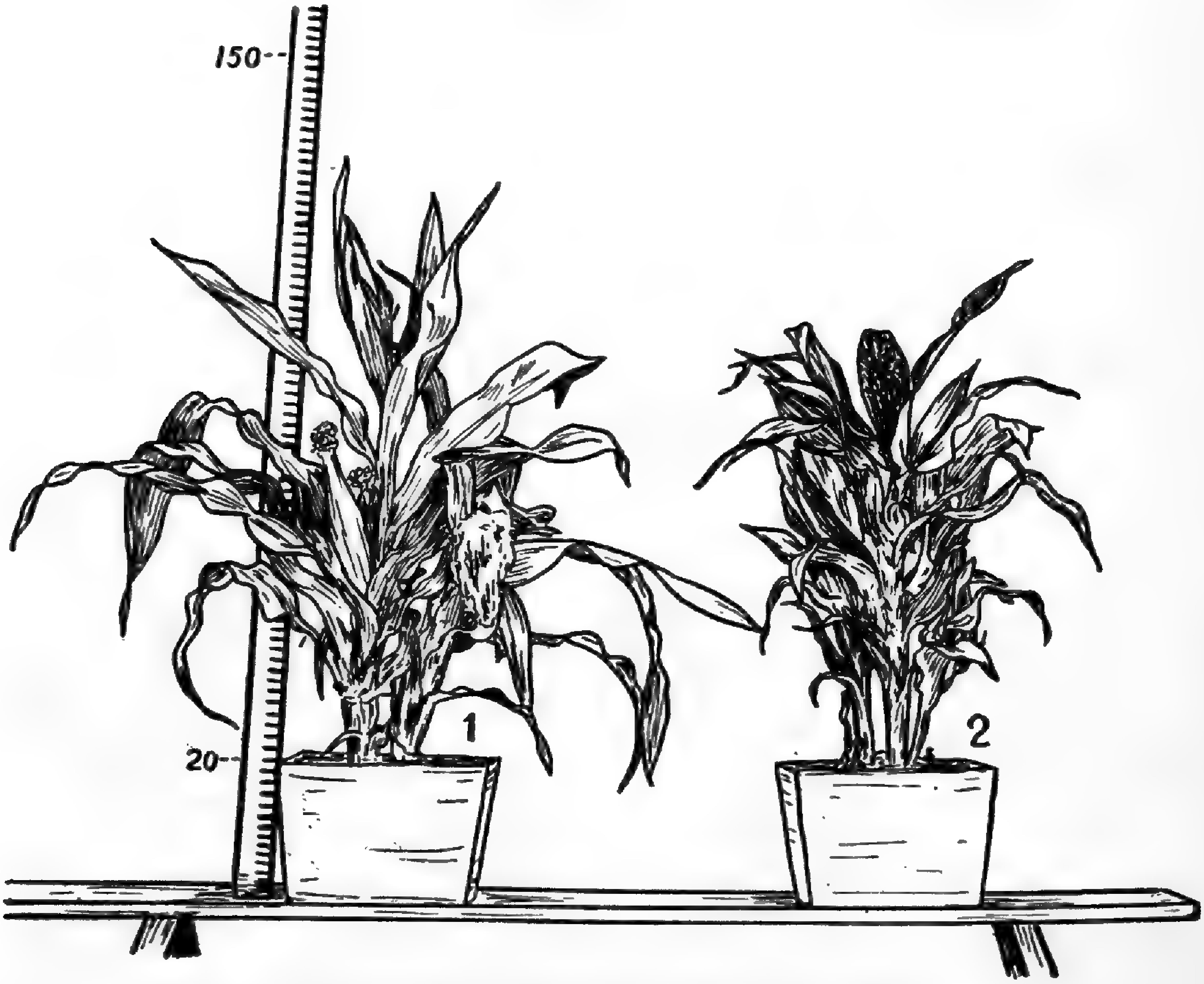

Fig. 12. Sorghum and maize plants of short habit, from Bokhara, 1927.

already quite striking in appearance at the 9–10-leaf stage, being sufficiently distinguished by tall plants with thin stems, long basal internodes, and a palm-like arrangement of their long, narrow leaves at the apex (fig. 13). These plots all contained plants from Manchuria, northern China, and the Primorskiĭ Province. Further observations showed that, besides sorgo and maize, the same plant structure may be observed in plots of *Panicum italicum* from the same regions.

Upon further development the similarity between these plants is not diminished: Manchurian Kaoliang resembles Manchurian and Primorskiĭ maize, and Manchurian and Primorskiĭ maize are similar in aspect to Kaoliang. Figure 14 represents maize and sorgo from central and eastern Asia, photographed after flowering. The similarity is striking. In these two regions sorgo and maize are so similar in external aspects that an inexperienced observer recognized sorghum plants of these regions by their outward aspect without difficulty, after once seeing our plots of the peculiar maize of central and eastern Asia. In addition to the illustration, we present measurements of the internodes of the plants which were photographed, numbering the internodes from bottom to top (Table IX).

The data presented here corroborate well what was stated in the text and demonstrated in the illustrations. The facts which have been studied in this section lead involuntarily toward the raising of several general questions of the biology and variation of plants. For instance, *Andropogon sorghum* presents an Asiatic

TABLE IX

INTERNODE LENGTHS (IN CM.) IN PLANTS OF SORGHUM AND MAIZE IN FIG. 15, GROWN AT KHARKOV, 1927

Number of internodes	Sorghum Bokhara	Maize Termez	Manchuria	
			Sorghum	Maize
1	2.0	2.0	4.0	6.0
2	2.5	3.5	11.0	8.0
3	3.75	4.0	21.0	8.5
4	3.75	6.5	27.5	20.0
5	4.0	3.25	24.5	22.5
6	4.5	5.5	24.5	19.0
7	4.0	4.0	27.0	21.0
8	4.0	3.3	29.5	18.5
			(to panicle)	
9	5.0	5.0	49.5	18.0
10	5.0	4.5		
11	5.0	10.0		
12	5.0 (to panicle)	9.0		
13	15.0	8.0		
14		2.0		
15		1.5		
16 (to panicle)		8.0 (to panicle)		
17		9.0		

aspect, having been known to be in culture in Asia for more than 3,000 years. Also maize, according to the present view, could not have been introduced into Asia earlier than 1516, when the Portugese ships first touched the China shores. Thus, 400 years is the maximum time which, on the basis of the literature, can be assumed for the cultivation of maize in Asia. In an evolutionary sense it is impossible to consider 400 years a long time, but meanwhile, during these 400 years, maize, which is foreign to the Asiatic continent, attained an aspect similar to that of the oldest crop plant in Asia—sorgo. On the basis of these observations we must assume either a very high plasticity for the maize plant, or conversely, that maize was introduced into Asia earlier than 1516. Unfortunately, due to insufficient data, the latter is an impossible assumption.

4. LIGULELESS MAIZE

A peculiar condition of leaves which lack a ligule at the juncture of the leaf sheath and the blade has been described in cereals by several authors. Nilsson-Ehle observed it in oats; N. I. Vavilov discovered liguleless type of rye and wheat in Pamir; K. A. Flaxberger established the presence of liguleless wheats in collections from the island of Cyprus (Flaxberger, 1926). Liguleless maize was described by Emerson (1912). Liguleless plants were discovered by him in 1910 in the progeny

Fig. 13. Similarity of plant habit in sorghum, maize, and *Panicum italicum* from Manchuria, in the 9- to 11-leaf stage. [From left to right]: maize, *P. italicum*, sorghum. Kharkov, 1927.

of a self-pollinated plant which was grown from a single ear with tooth-like kernels which was brought from the National Corn Show in Omaha. A closer inspection of the leaves of the *liguleless* plants showed that, besides the reduction of the ligule (which in several leaves is retained although in a very rudimentary form), the auricles, by which the vertical position of the leaves and their clasping of the stem is actually accomplished, are also absent.

A genetical investigation of the character *liguleless* demonstrated that it is recessive and in hybrids segregates in a ratio of 3:1. As fas as we know, no one besides Emerson has studied the character of ligulelessness in maize. In 1927 at Kharkov in our plots, V. I. Savron and I discovered ligulelessness in plants of maize in three cases:

Fig. 14. Convergence in vegetative habit of maize and sorghum from central and eastern Asia. Center, a plant of *P. italicum* from Manchuria. Kharkov, 1927.

1. *Collection no. 2773 from the village of Seraphimovok, the Vladivostok district in the Primorskiĭ Province, referred to the group everta.* Among 20 plants of a plot, in 11 the leaves on different stems were marked by a reduction of the ligules from complete absence to its retention as a rudiment as compared with the normal aspect. The auricles were absent from the leaves. In fig. 16 this original plant type is depicted.

2. *Collection no. 2746 from the village of Novopokrovok, in the Spassk district, the Primorskiĭ Province.* Of 22 plants only one was liguleless, but the ligulelessness was very well developed.

3. *Collection no. 1419, originating from the Caucasus (unfortunately without a more exact notation as to place, and doubtful as to origin).* Of four plants, one was typical liguleless.

Liguleless plants were not discovered in any other collections either at Sukhum or Kharkov, notwithstanding the fact that the collection was world-wide. Also, in general, no one has established ligulelessness before in open-pollinated collections of maize under natural conditions of development. Our findings appear to be peculiar in their class and the maize of Asia is of new interest.

Collections nos. 2773 and 2746 were received from the Primorskiĭ Province the first of the year 1927, and were first seeded in 1927. The origin of collection no. 1419 is not certain, but the original seed of it was used for sowing.

Fig. 15. Maize and sorghum stems with the leaf sheaths removed, from Bokhara and Manchuria. Kharkov, 1927.

Fig. 16. Liguleless plant in collection 2773 from the Primorskiĭ Province, near Vladivostok. Kharkov, 1927.

III. GENERAL CONCLUSIONS CONCERNING THE MAIZE OF ASIA

In the preceding section, on the basis of data from the literature and from our own investigations, we arrived at the conclusion that in the maizes of Asia we have observed an array of characters and peculiarities which are unknown in America, or which are extremely rare in America. At any rate, we observed these characters, not in occasional isolated instances but often and associated with definite and frequently large areas. Therefore, waxy endosperm has a wide distribution in eastern Asia from 5–45° north latitude; dwarf plants are peculiar to vast areas of central Asia; while the sheltering of the panicles by the upper leaves and the concealment of the silking ears in the leaf sheaths are encountered in eastern and central Asia, Transcaucasia, etc.

These facts indicate that in Asia several conditions contribute to the production of new types of this plant which is known to be American. However, when we appraise more closely the characters which are peculiar to the maizes of Asia or discovered in them, we should, on the basis of the data from the literature, meet recessiveness in most of them. Thus waxy endosperm, *brachytic* dwarfness of the plant habit, and ligulelessness are recessive.

In 1927 N. I. Vavilov published a very interesting work on the geographical regularity in the distribution of genes of the crop plants. In the words of N. I. Vavilov: "The basic centers of diversity of types are the sources of diversity which are characterized not only by the presence of a large number of types, but, what is no less important, by the presence of a large number of dominant factors. Conversely, the secondary centers of diversity are characterized by a diversity principally of recessive factors."

From this viewpoint concerning the maize of Asia we undoubtedly have a secondary center of diversity, and our Asiatic material gives satisfactory facts for the corroboration of the views of N. I. Vavilov. At the present time no one doubts the American origin of maize (Messedaglia, 1924; Weatherwax, 1923) [And a reference to a non-existent sixteenth item in his *literature cited*], and the Asian maize is of course viewed as an introduction.

This assertion by no means hinders the raising of another exceedingly interesting question, and this question concerns the time of introduction of maize into Asia. At present we have no documentary evidence which would indicate that maize was known in Asia before Columbus [A reference to a non-existent seventeenth citation]. But the striking facts which are described in the present paper inevitably lead to the idea that Asian maize, if it be not viewed as native, at any rate is very ancient. These characters, which were seen in Asiatic maize, attest to this explanation. As we saw, waxy endosperm, which was discovered in Asiatic maize, was also discovered in the most ancient crop of Asia—sorgo. Dwarfness, which is characteristic of Asiatic maize, is also characteristic of sorgo, flax, and other ancient crops. But these characters are found in large areas, and for them to be manifest in maize, time, of course, is required.

If we agree with Collins, we must assume that waxy endosperm arose in the maizes of Asia by means of mutation and has its place of origin in upper Burma, which is largely populated by wild tribes with whom even today it is almost impossible for aliens to have intercourse. Now, concerning the time interval in question, we must understand when and how maize could have been removed from America into this isolated wild land, given there a mutation and as a mutant diffused from the Philippines to northern Manchuria. The answers we can not give, of course, with certainty, but as a conjecture we should suppose that likely there was an earlier cultivation of maize in Asia than the time of the first landing by the Portugese on the shores of Asia in 1516. A similar conjecture was expressed in one of his papers by Collins (1909), but subsequently he retracted it. The facts, which were established by us, return us anew to this supposition and this time with a great deal of conviction.

We have already dwelt upon the agricultural and biological significance of these characters which were described for Asian maize. Their value as to suitability to the exceptionally dry conditions of central Asia is undoubted, and therefore Asiatic maize arouses a very great interest regarding plant breeders' aims. The character *waxy* is no less interesting from the practical point of view. The exceptional capacity of waxy endosperm to be hydrolyzed by the diastase enzyme has been explained according to the most recent investigations of Americans. In comparison with other types of endosperm, the hydrolysis of waxy endosperm is more rapid in several cases [Reference to literature citation 18].

This condition leads one to suppose an increasing adoption of the products prepared from waxy maize in the diet of the natives. We do not yet know the suitable experiments, and we know nothing about the conduction of plant-breeding experiments with waxy maize, but both [questions] arouse very great interest.

Rapid-growing races of waxy maize from the Primorskiĭ Province and northern Manchuria ripened fully under the conditions of Kharkov, and subsequently in almost the entire maize-growing region of the USSR.

The present communication represents in part the large cooperative work on the investigation of maize and sorgo which is being conducted by the author in cooperation with I. V. Kozhukhov, M. I. Hajinov, V. I. Savron, A. I. Ivanov, and E. S. Yakushevskii at the All-Union Institute of Applied Botany. We must also mention the exceptional aid which was rendered by the section of M. G. Tsyup in photographing the most interesting plants. We express also our deep gratitude to all the institutions and persons who responded to the requests of the section and sent to the Institute collections which served in a large part as material for the present paper.

Leningrad.

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LADYFINGER AND TOM THUMB, TWO OLD VARIETIES OF POPCORN

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Two very different varieties of popcorn, Ladyfinger and Tom Thumb,[1] have been extensively confused in agronomic and genetic literature. While the correct naming of popcorn varieties is a matter rather outside the ordinary realm of scientific endeavor, these two varieties have been so frequently used in genetic and breeding experiments, East (1911), White (1917), and Kempton (1926), that it seems worth while to describe and differentiate them. Aside from small kernels and small cobs the two have almost nothing in common. Each represents a morphologically extreme type among the readily available United States varieties of *Zea Mays;* for that very reason both may be of potential importance in practical breeding programs as maize breeding becomes even more scientifically expert.

A few of the outstanding differences between these two varieties are shown in Table I. Even though the varieties have been confused because both have small ears and small kernels, they are readily distinguishable even by these characters. Ladyfinger has smaller kernels than does Tom Thumb and they are a straw-yellow rather than a butter yellow. The ear of Ladyfinger does indeed suggest a finger, being slender and straight-sided, while the ear of Tom Thumb, though usually even shorter, tapers from the center to both ends, like a miniature barrel.

In growth habit the two varieties are diametrically different. Tom Thumb is the earliest of early varieties and does not grow into a normal plant south of the northernmost tier of states. In most of its characters it is a typical northern flint (Brown and Anderson, 1947). It has one or two ears on the main stalk when grown in southern Minnesota. It tillers readily and the tillers are inferior to the main stalk. The foliage is a yellowish-green and the tassel has few and slender branches. Ladyfinger is the latest variety of any kind of maize in most of the gardens in which it grows. Its growth habit is like that of Oriental Popcorns (Stonor and Anderson, 1949): it develops slowly; its leaves are upright; the internodes are short; it may have 5 to 7 ears on the main stalk. It tillers abundantly and the tillers are subequal to the main stalk in size and appearance (pl. 12, fig. A). The tassel, though small, has many branches and is scarcely exserted from the upper leaves.

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[1] In discussing these two varieties we have used the oldest names in the literature, the more readily since they are appropriate names and since they have been widely used for these varieties at one time or another. Ladyfinger has been very extensively referred to, not only as Tom Thumb but as Australian Hull-less. The latter name, however, seems to have been even more widely applied to varieties which apparently came from crosses between Ladyfinger and some variety with a higher row number. The name Tom Thumb has been applied not only to Ladyfinger but also to various small-eared popcorns, including pointed-kernel types which morphologically are very different from the Tom Thumb herein described.

TABLE I

TABULATION OF OUTSTANDING DIFFERENCES BETWEEN TOM THUMB AND LADYFINGER POPCORNS

	Tom Thumb	Ladyfinger
Season	Very early	Very late
Ear shape	Small, barrel-shaped	Small, finger-shaped
Kernel color	Deep yellow	Pale yellow
Tassel	Few branches; exserted from leaves	Many branches; tassel surrounded by upper leaves
Leaves	Yellowish-green	Bluish-green, upright
Internodes	Few; upper ones elongated	Many; upper internodes very short

Little is known of the history of either variety though both have been commonly grown under various names and both have been used in popcorn breeding for over fifty years. Eldredge (Eldredge and Lyerly, 1943) described both varieties as among the types of Tom Thumb popcorns which he found when assembling material for his popcorn-breeding program.

Though little is known about the agronomic history of Ladyfinger the facts suggest that it may be one of the oldest varieties of maize. It is strikingly similar to varieties of popcorn obtained from pre-Columbian graves in Chile and Peru. Varieties somewhat resembling it have been obtained from scattered localities in South America and, as mentioned above, it is generally similar to the popcorns collected among the primitive Naga tribes of Assam by Stonor. Though we do not know how or when it reached the United States, we do know that it has been here over a century. A detailed description of it by Ebeneezer Emmons in 1849, leaves no room for doubt that it was this very same variety to which he gave the name of Ladyfinger in his survey of the maize varieties in New York State (p. 265):

> "Illinois or Ladyfinger corn. Pale yellow. Ear small, slender, and tapering. Rows 12. Kernels small, pointed, rounded upon the back. It is an unproductive kind, bearing sometimes four ears upon a stalk, but the stalk is from 7 to 8 feet high. It is a late kind . . . ."

Ladyfinger is a high-quality popcorn. Though small and comparatively flavorless, it is delicate in texture and is almost completely devoid of the roughage which some people find so objectionable in most other popcorns. It is this high quality which has preserved it in spite of its lateness and rather low yield. We have frequently found it being grown by small seedsmen or in home gardens. Inquiry as to where it had been obtained has always produced a similar story. Some friend or relative found it to be of such high quality that it was recommended as being worth while in spite of its lateness. In the few cases where we were able to go back one step farther we learned that the previous grower had himself obtained it in just such a fashion.

Ladyfinger has evidently been used considerably in popcorn breeding. We found the first-generation hybrid between it and Japanese Hull-less types to be high both in quality and yield. Various blends of the two varieties are, or have been, under cultivation but those which we have grown show a strong tendency to revert back to the original Ladyfinger type.

About Tom Thumb we know even less. In its growth habit it is so similar to the early small-eared northern flint varieties such as those grown by the Micmac Indians that it would seem to be either a northern Indian variety or one produced by crossing some other popcorn with one of these varieties.

In our collections are specimen ears, some of them going back to the first decade of the twentieth century from several localities in eastern north America. Modern popcorn breeding has driven it almost out of existence. From Professor Wiggans of Cornell we obtained a very early inbred derived from this variety or one of its hybrids. We were not, however, able to obtain viable seed of the open-pollinated variety until we finally located a stock at the Montreal Botanical Garden where the superintendent, Henri Teuscher, had been growing it for some years. Because of its scientific value this was increased for us by William Landgren of Willmar, Minnesota, and will be generally available for scientific or practical experiments.

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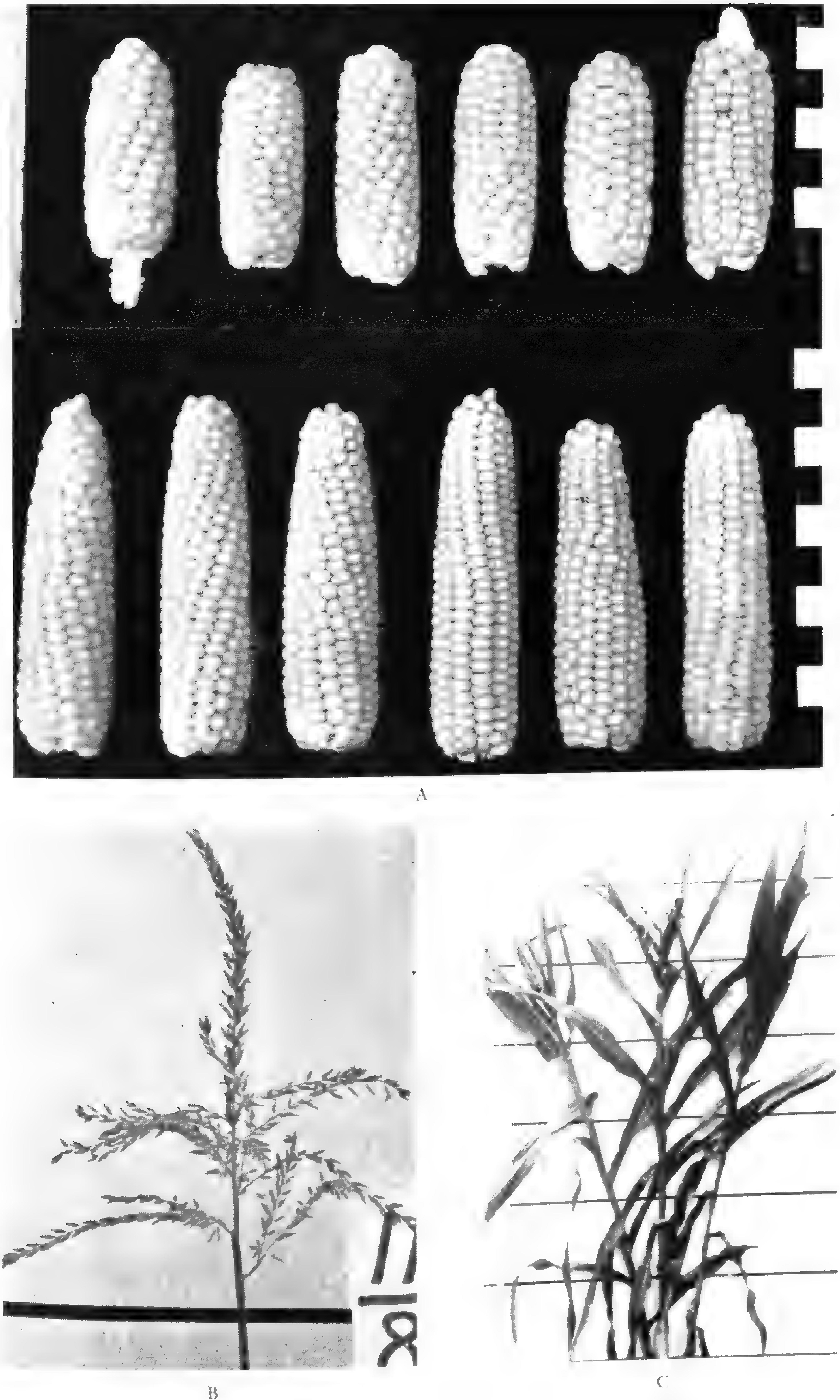
Explanation of Plate

PLATE 12

Fig. A. Above, 6 ears of Tom Thumb; below 6 ears of Ladyfinger. Scale at the right in centimeters.

Fig. B. Close-up of tassel of Tom Thumb. Line is the same width as those in the background of Ladyfinger illustration.

Fig. C. Typical plant of Ladyfinger. Tracing of leaf blade at the left. Background ruled in lines 25 cm. apart.


A

B C

ANDERSON AND BROWN—OLD POPCORN VARIETIES

A FIELD SURVEY OF CHROMOSOME NUMBERS IN THE SPECIES OF *TRADESCANTIA* CLOSELY ALLIED TO *TRADESCANTIA VIRGINIANA*

EDGAR ANDERSON

PART I. PRESENTATION OF DATA

Some twenty years ago I began to collect quantitative data on variation in chromosome number in *Tradescantia.* Having learned at the John Innes Horticultural Institution the comparative ease with which accurate chromosome counts of the American Tradescantias could be made with modern methods, and living within easy-collecting distance of five different species, I set about to supplement the extensive chromosome-number surveys of various other cytologists by an intensive survey of a few species. Darlington (1929) had shown that chromosome number *could* vary in this group of species; I thought it would be productive to learn to what extent it actually did vary. This eventually led to taxonomic (Anderson and Woodson, 1935) and cytological monographs (Anderson and Sax, 1936) with Dr. R. E. Woodson, Jr. and with Dr. Karl Sax in which I undertook the major responsibility for building up a comprehensive collection of living plants while my colleagues performed the bulk of the technical investigations. When still actively engaged upon the survey I stumbled upon the phenomenon of introgression. Before the survey was completed I had moved from the Missouri Botanical Garden to Harvard University and then moved back again. In spite of these diversions the survey has proceeded. Chromosome numbers have been carefully determined for nearly 1000 plants of eighteen species of *Tradescantia* in the *virginiana* group, all of them collected in the field. Nearly 500 of these counts have been accurately recorded and filed and are presented herewith. They give good, quantitative data on the stability of chromosome number under field conditions. Preliminary accounts were included in the cytological and taxonomic monographs, and a summary of some of the main points was included in a survey article in the *Botanical Review* (Anderson, 1937). Detailed reports have been made on various special phases of the investigation (Anderson, 1936; Anderson and Diehl, 1932; Anderson and Hubricht, 1938; Riley, 1936; Whitaker, 1939). This constitutes a final report on the original project. In presenting the cytological data for each species, I have therefore included additions and corrections to the cytological and taxonomic monographs, as well as notes and comments on each species as an evolutionary unit.

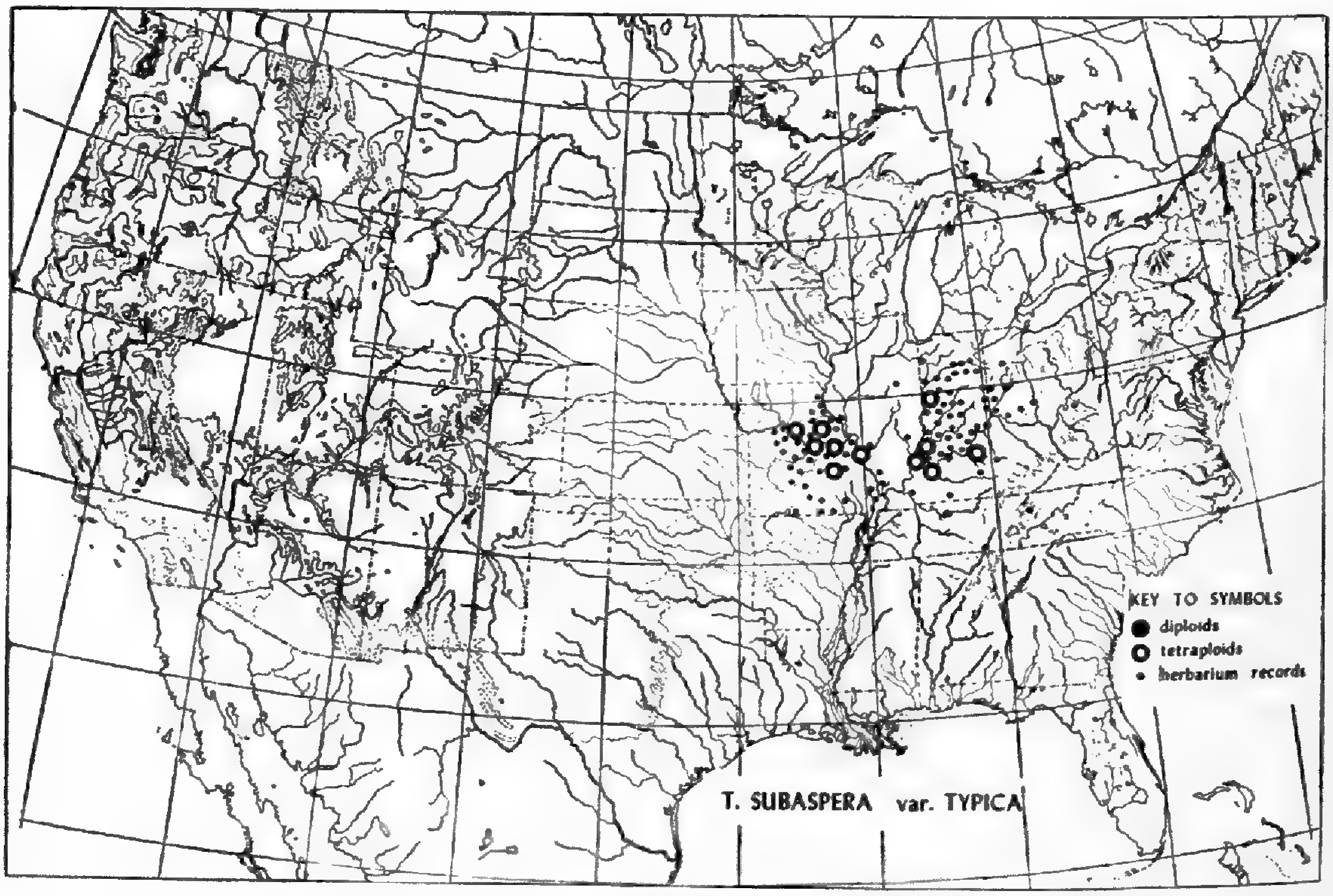
METHODS

Counts were made both in the field and the experimental plot. They were made almost exclusively from fresh aceto-carmine smears. Wherever possible metaphases of both meiosis and mitosis of the microspores were examined. Any seeming irregularities of either of these divisions were exhaustively looked into. If the microspores showed any micronuclei or if the percentages of sterile pollen were higher than normal, meioses were obtained for study even though this meant transplanting to an experimental plot and re-investigating the plant in another season.

Counts were made in the field or on transplants of my own collecting and on plants sent in by friends and collaborators. The technique of labelling and indexing these collections has been described in detail in Anderson and Sax (1936).

Presentation of Data

The species are presented here in the same order as the taxonomic monograph by Anderson and Woodson: *T. subaspera, T. edwardsiana, T. ozarkana, T. ernestiana, T. virginiana, T. hirsutiflora, T. tharpii, T. gigantea, T. ohiensis, (T. reflexa, T. canaliculata), T. paludosa, T. bracteata, T. hirsuticaulis, T. longipes, T. reverchoni, T. humilis, T. subacaulis, T. roseolens, T. occidentalis.* These are all in the *virginiana* group and represent all the known species of that group native to the United States. They all have erect or ascending stems, not ordinarily rooting at the nodes (see comments under *T. paludosa*). The sepals are more or less concave but are without a definite keel. The bracts below the flowers are conspicuous and similar to the leaves. The seeds are somewhat oblong with a linear funicular scar as long as the seed. The chromosomes are large with median or submedian attachment constrictions. The chromosome number (2n) is normally either 12 or 24.



Map 1

***Tradescantia subaspera* var. *typica*.—**

This has been sampled at twelve localities from northern Florida to central Missouri. At Wolf Creek, in eastern Tennessee, one diploid (2n = 12) was collected. The 16 other plants, from the eleven other localities, were all tetraploid

(2n = 24). No plants were found with extra chromosomes, with fragment chromosomes, or other cytological abnormalities.

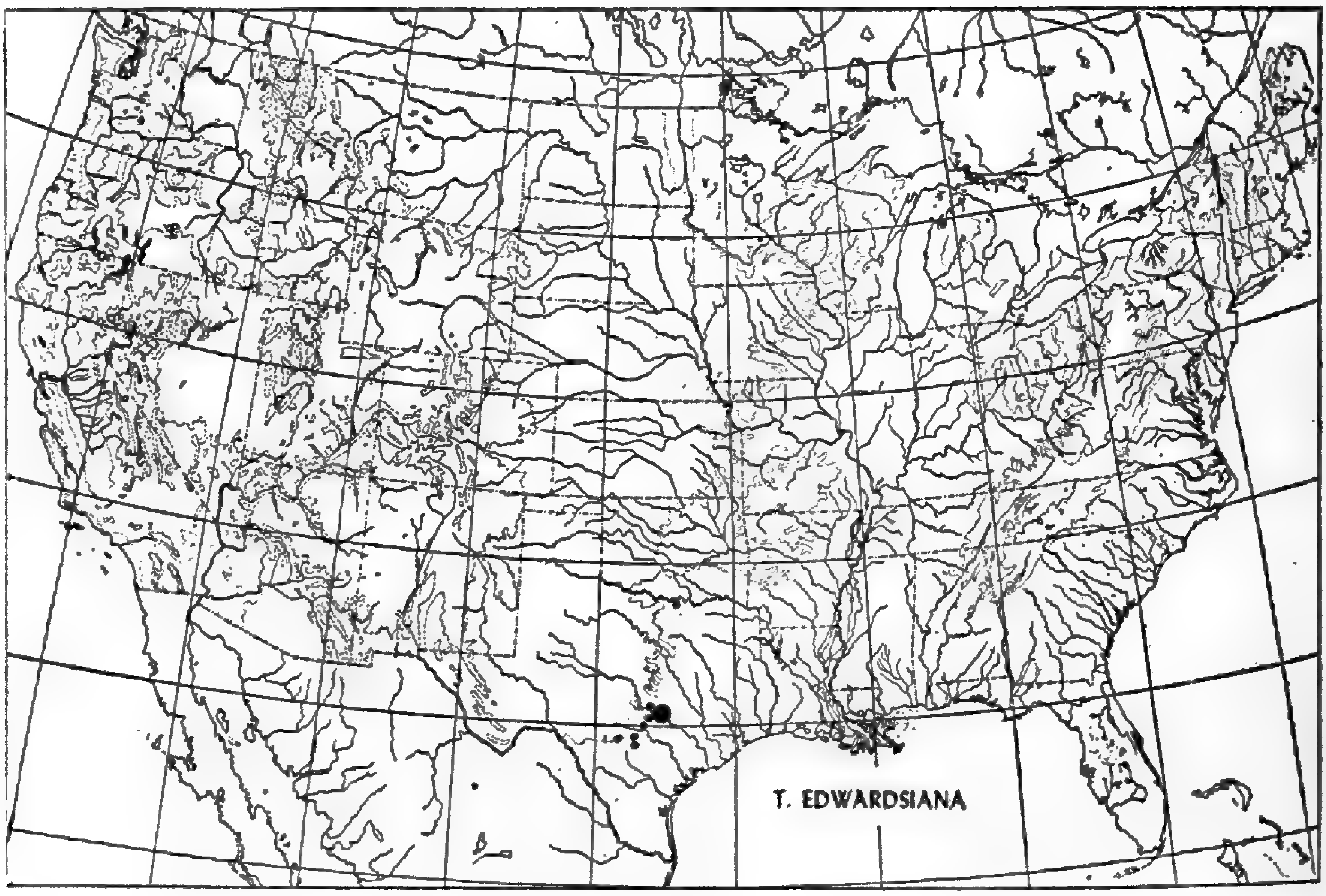
T. subaspera var. *typica* is a handsome, summer-blooming plant of deep shade and rich soils which in its general appearance is quite unlike the other species of this group. The record in northern Illinois in Anderson and Woodson was in error. The common so-called *T. virginiana* of gardens is descended almost as much from this species as from true *T. virginiana*.

Map 2

Tradescantia subaspera var. *montana*.—

Morphologically, this variable taxon is similar to artificial hybrids between *T. subaspera* var. *typica* and *T. ohiensis*. Hybridization with the latter species is still actively going on, particularly in habitats grossly disturbed by man, and two of these are reported below. *T. subaspera* var. *montana* is so variable and has so much higher a percentage of sterile pollen and cytological abnormalities than any of the other taxa reported on here, that it seems likely it is the result of introgression of *T. ohiensis* into *T. subaspera* var. *typica*. Though much of this introgression may have occurred recently it was the opinion of Dr. Hiram Showalter, who was studying the phenomenon at the time of his death, that part of it was pre-Columbian. A careful study of *T. subaspera* var. *montana* in the field and in the breeding plot would settle this question and be of general interest. I have Dr. Showalter's notes and herbarium specimens, as well as a few of my own, and shall be glad to turn them over to any qualified person with the facilities for continuing with the problem.

Collections were made at eight localities, from Alabama to Tennessee and North Carolina. Chromosome counts were made on 25 plants in all. Twenty-four of these were regular tetraploids with 24 chromosomes. The other plant had two extra chromosomes; it showed a high percentage of bivalents at meiosis; and the microspores contained occasional micro-nuclei.



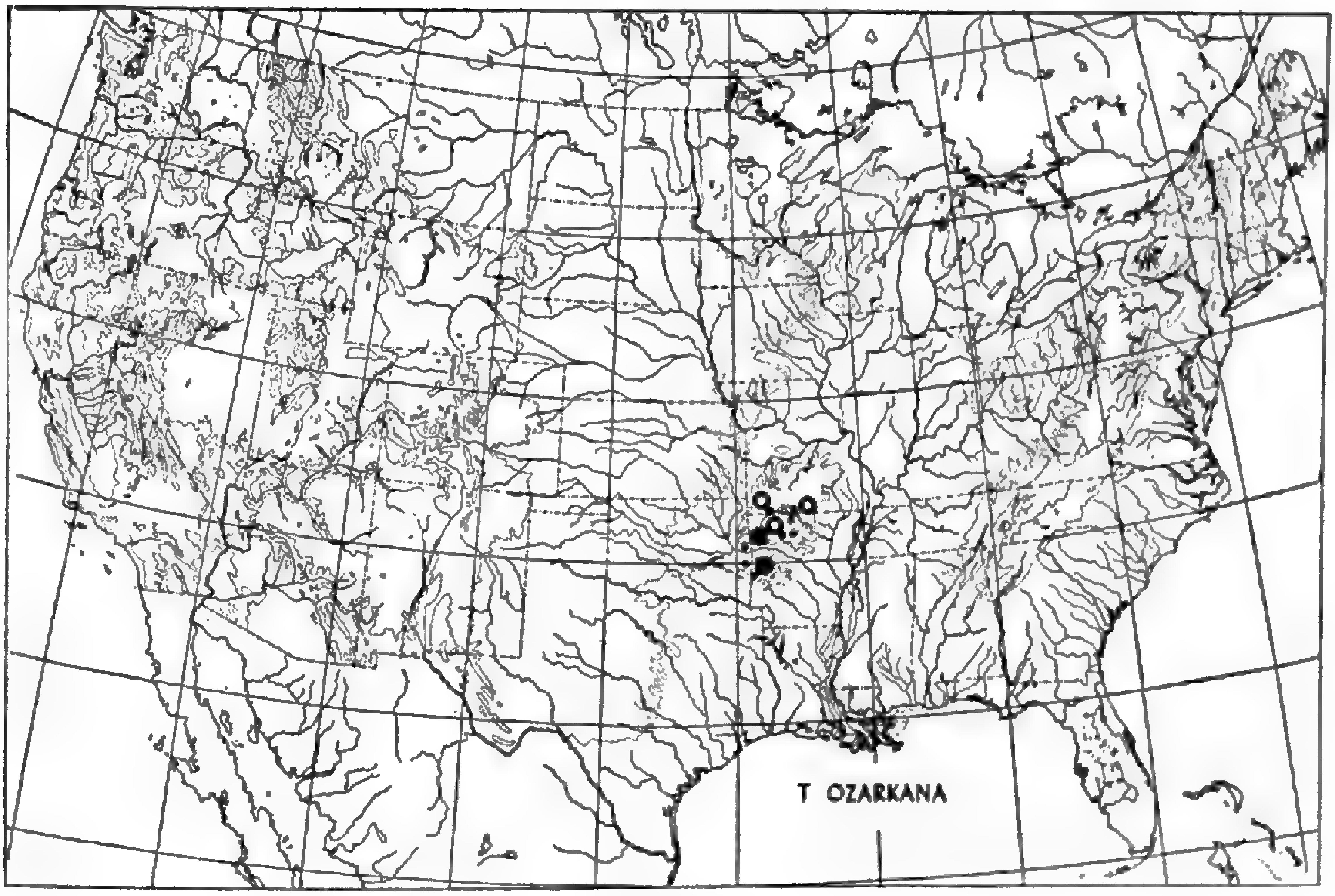
Map 3

Tradescantia edwardsiana.—

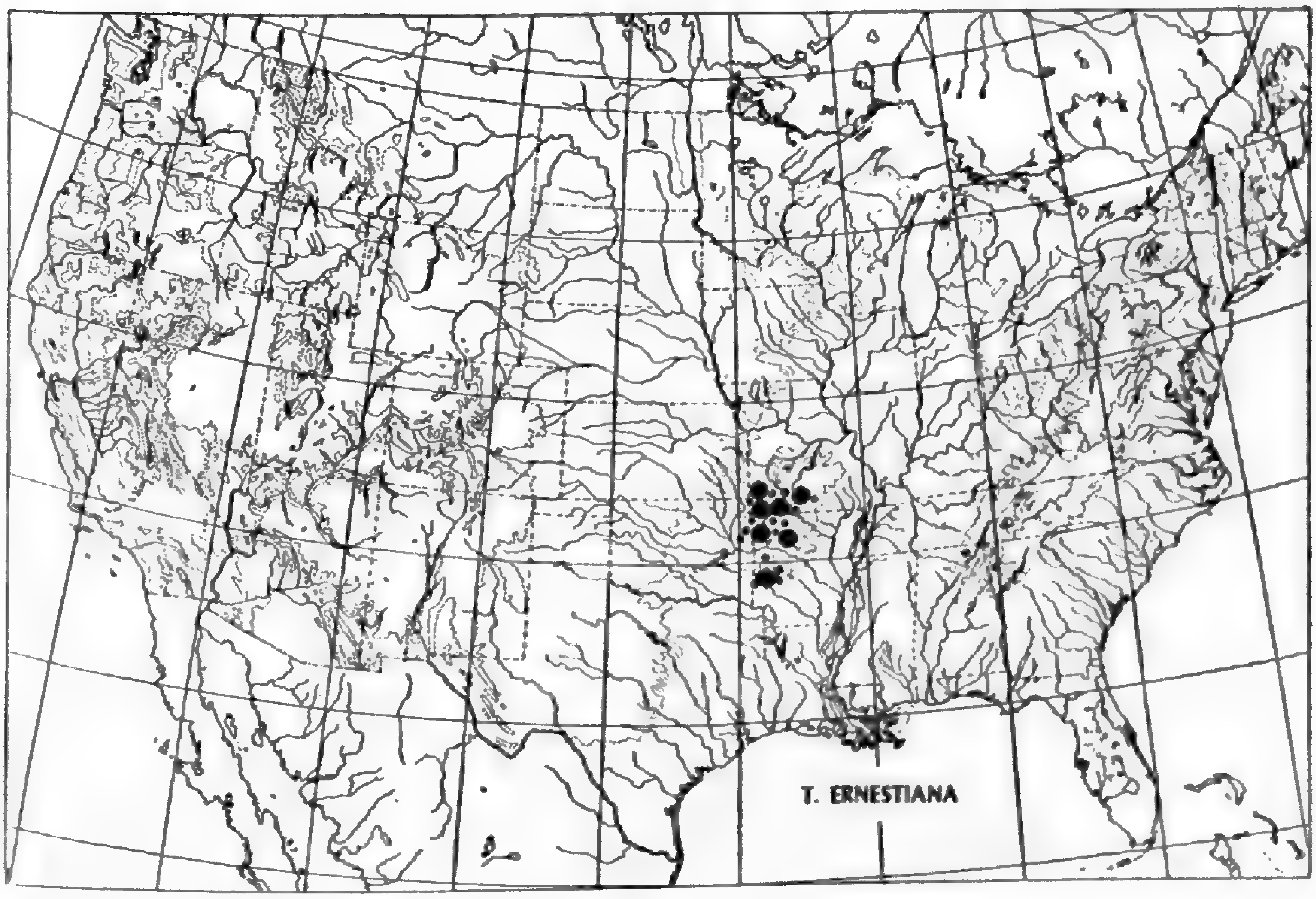
This is a very localized species growing in shady spots along the edge of the Edwards Plateau. Additional collecting has extended the range to northern Texas. Collections were made at two points; 17 plants were examined. All were regular diploids with 12 chromosomes.

Tradescantia ozarkana.—

This peculiar species has a disjunct distribution on isolated Cretaceous mesas and plateaus in Arkansas and southwestern Missouri. Additional collecting has slightly extended the range. At the most southwestern part of its range (Rich Mountain) this species is diploid. In the Boston Mountains and in the Ozarks it is a tetraploid. Counts were made on one plant each from five localities. All were regular tetraploids or regular diploids with no extra chromosomes or other cytological abnormalities. In southwestern Missouri, at the type locality for the species, it is undergoing extensive introgression from *T. ohiensis.*



Map 4



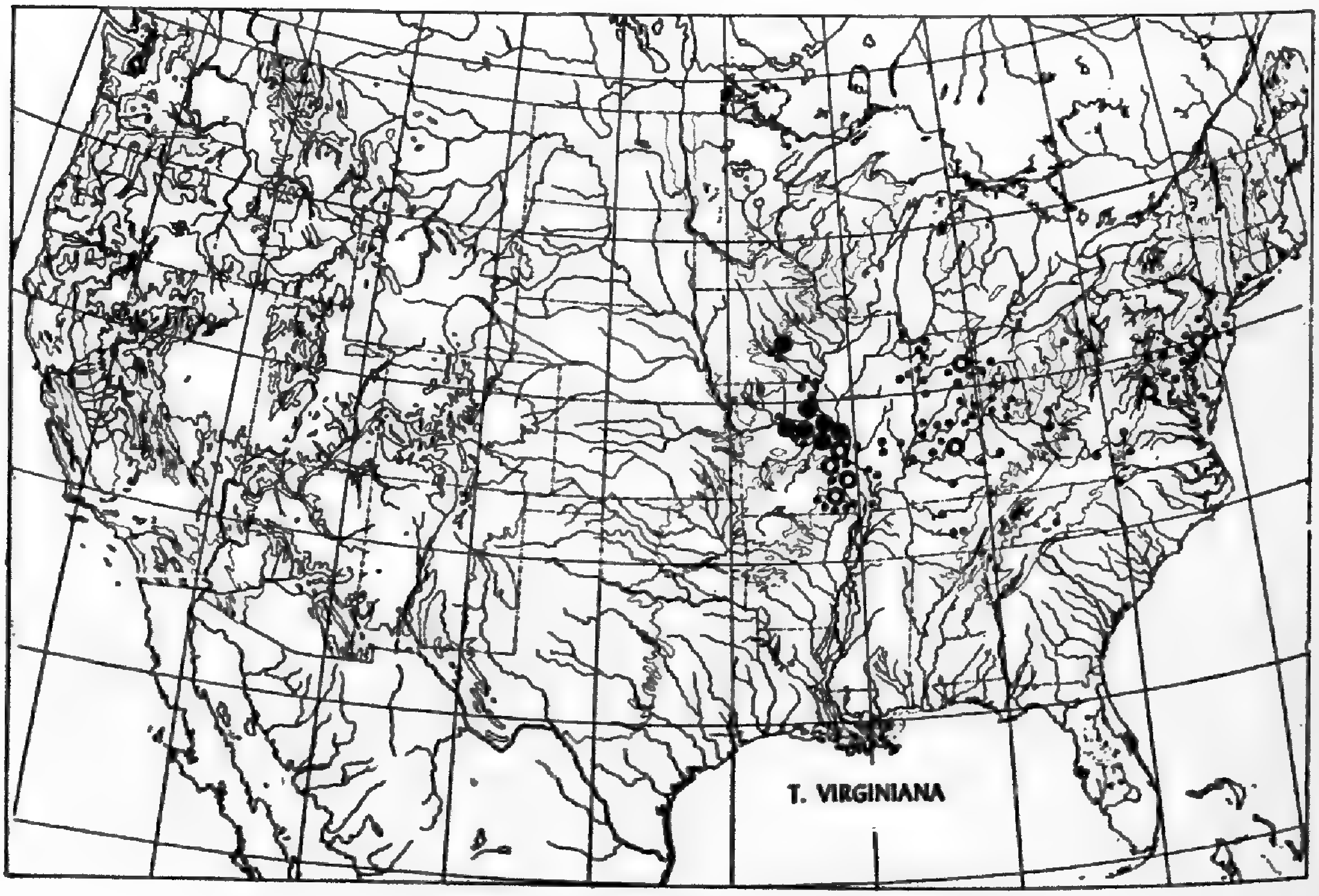
Map 5

Tradescantia ernestiana.—

This species is known only as a diploid. Nine counts were obtained at five localities from Rich Mountain to Missouri. All were regular diploids with 12 chromosomes (2n). *T. ernestiana* has a distribution similar to *T. ozarkana* though these two species are very unlike. Additional collecting and a better understanding of the species have extended the range to northern Alabama and northern Georgia, a range which is typical of many species found in the Ouachita Mountains. Specimen plants from northern Alabama sent us during the early years of our investigation by Dr. B. P. Kauffmann, and which we were unable to identify at that time, undoubtedly belonged to this species.

Tradescantia virginiana.—

During its career as a cultivated plant this species has been so modified by hybridization and selection that the plants now in cultivation under that name are completely outside the range of variation of the native populations of that species. This matter is discussed below at greater length. The previous record from Wisconsin is in error. The records from Michigan, Massachusetts, Vermont, and Maine are of garden plants run wild. The species is a regular tetraploid from Pennsylvania to southern Missouri. I have recorded counts on 16 individuals from eleven localities. One plant from De Soto, Missouri, was a tetraploid with 2 extra chromosomes. In the diploid area in northern Missouri and adjacent Illinois and Iowa we have counts on 18 plants from eleven localities. Seventeen of them are regular diploids; the other plant had 2 small fragment chromosomes which paired regularly at meiosis.

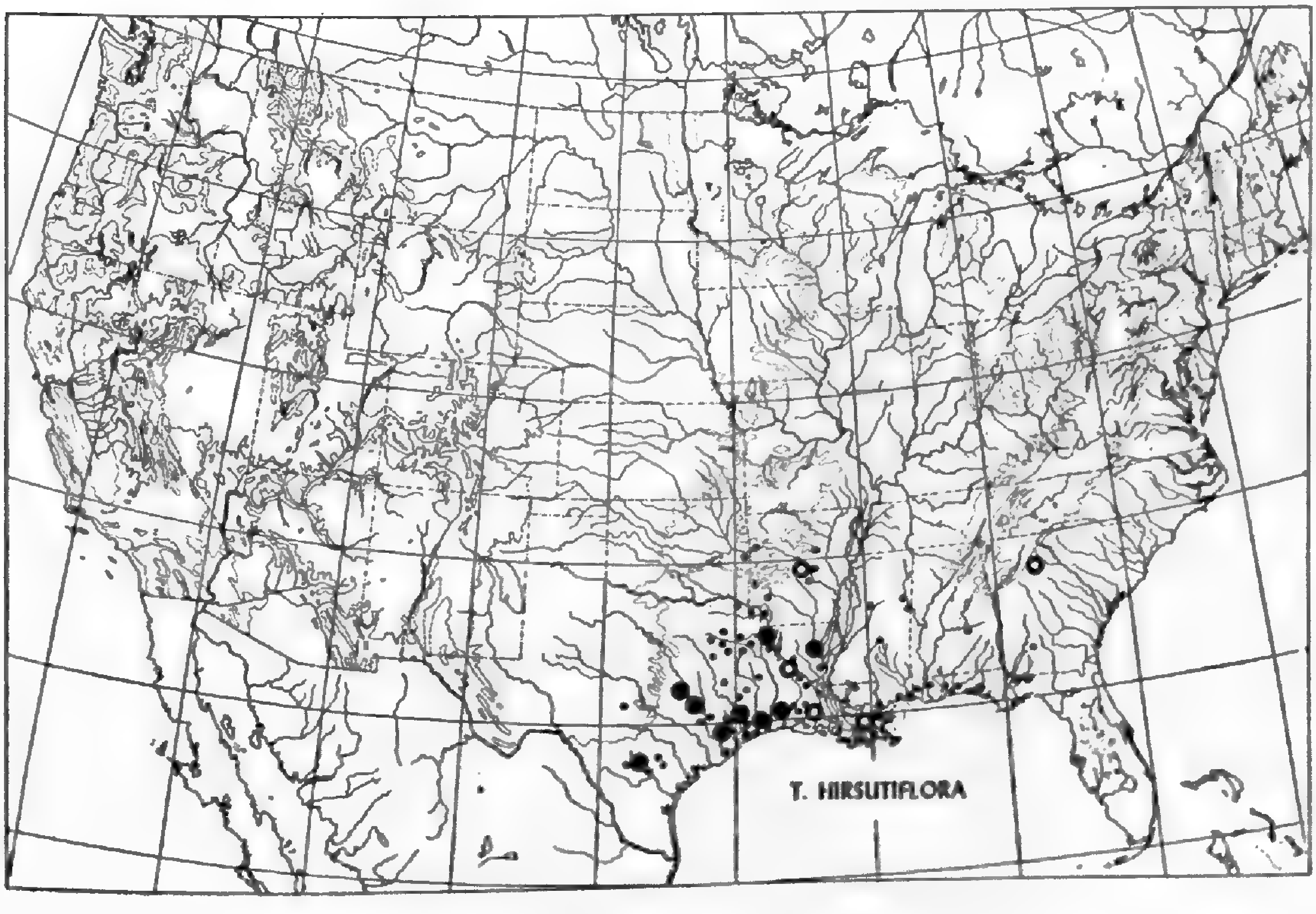


Map 6

The diploid zone of this now prevailingly tetraploid species is of some interest floristically. It includes the small area north of the Missouri River and west of the Mississippi which apparently was not over-run by either the Illinoian or Kansan glaciation. It is a region so rich in species which are rare or unknown in the glaciated areas immediately around it that Steyermark and others (Steyermark, 1934; Steyermark and Palmer, 1935) have supposed its floristic composition reflects its physiographic history. The fact that all the *T. virginiana's* which have been examined in this area are diploids, while the species is prevailingly tetraploid, would lend some support to this theory. The diploids, almost certainly the original form of the species, might have persisted here when eradicated elsewhere or their habitat might have retained its essential features here in the absence of glaciation though so altered in the glaciated areas that the diploids never spread back in.

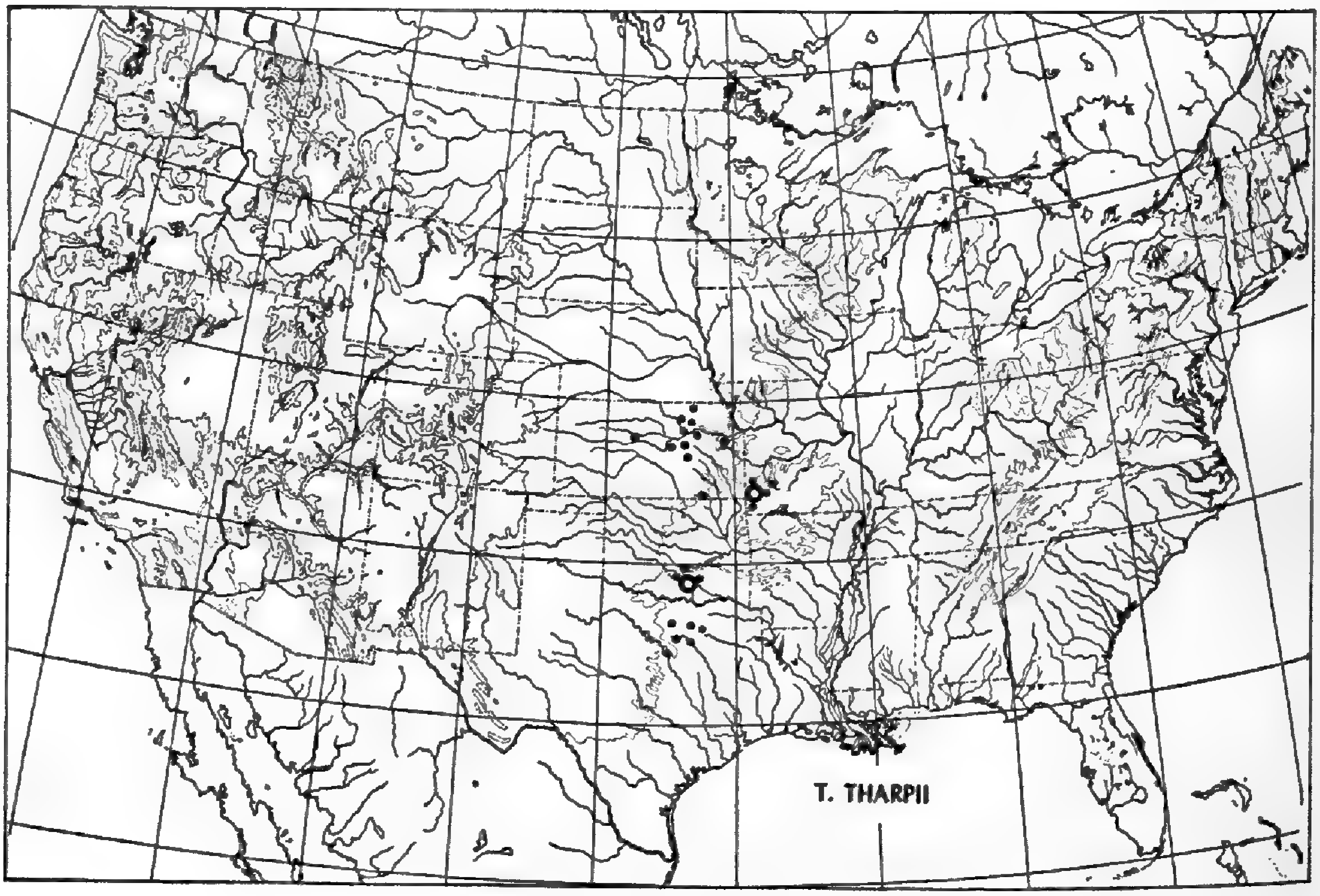
Tradescantia hirsutiflora.—

This is the least understood of any of the species in the *virginiana* group. Its members were originally native to light soils from Texas to Florida. Most of the habitats in which it originally flourished have been put under cultivation. Collections by Demaree have extended the distribution into central Arkansas. Introgression with several other species has taken place extensively, notably with *occidentalis, ohiensis,* and *paludosa.* Some of the introgressants are at a selective advantage in the new habitats, being under man's influence, and *T. hirsutiflora* is on its way to becoming a common weed in parts of the South. It, or something very closely akin to it, became incorporated in *T. bracteata,* forming a binary



Map 7

variation pattern which was the subject of a special study (Anderson and Hubricht, 1938). The weedy nature of *T. hirsutiflora* is reflected in the high percentage of cytological abnormalities which have been found in the relatively few populations which were examined. There is a diploid area in Texas and Louisiana, while as a tetraploid the species has spread north to central Arkansas and east to Georgia. The diploid has been studied at twelve localities. Twenty plants had no irregularities. Two had each an extra pair of chromosomes and one showed a large fragment chromosome at meiosis. Tetraploids were studied at four localities, one example from the same Louisiana parish as a known diploid. Chromosome counts were made on five plants. All were regular.



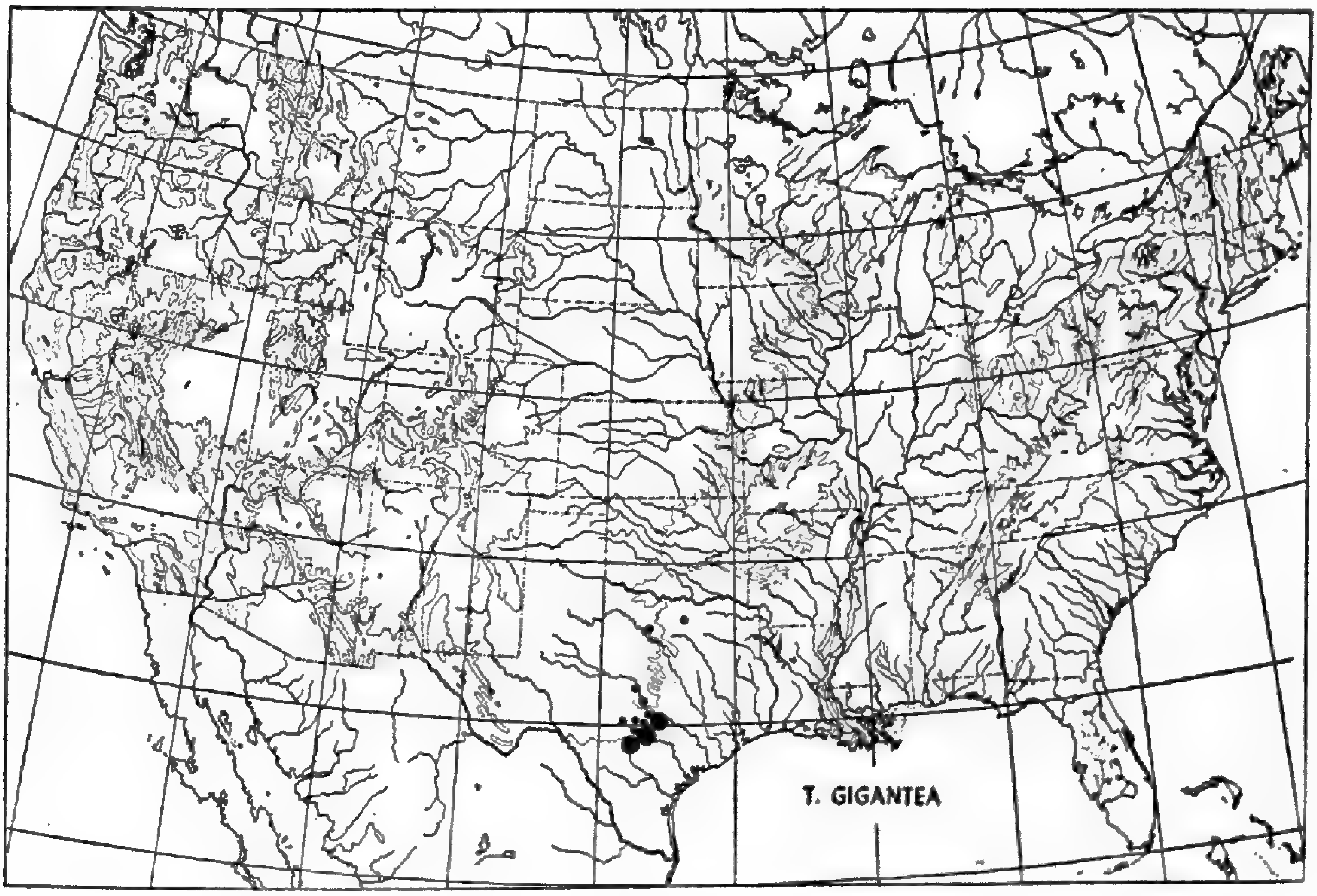
Map 8

Tradescantia tharpii.—

This charming and distinctive species is native to the front of the Great Plains from Texas to Kansas. The record from eastern Oklahoma (Anderson and Woodson, 1935) is in error. In addition to an early count from a plant collected somewhere in Texas, we have counts from one collection each in Oklahoma, southwestern Missouri, and Kansas. All seven plants were regular tetraploids.

Tradescantia gigantea.—

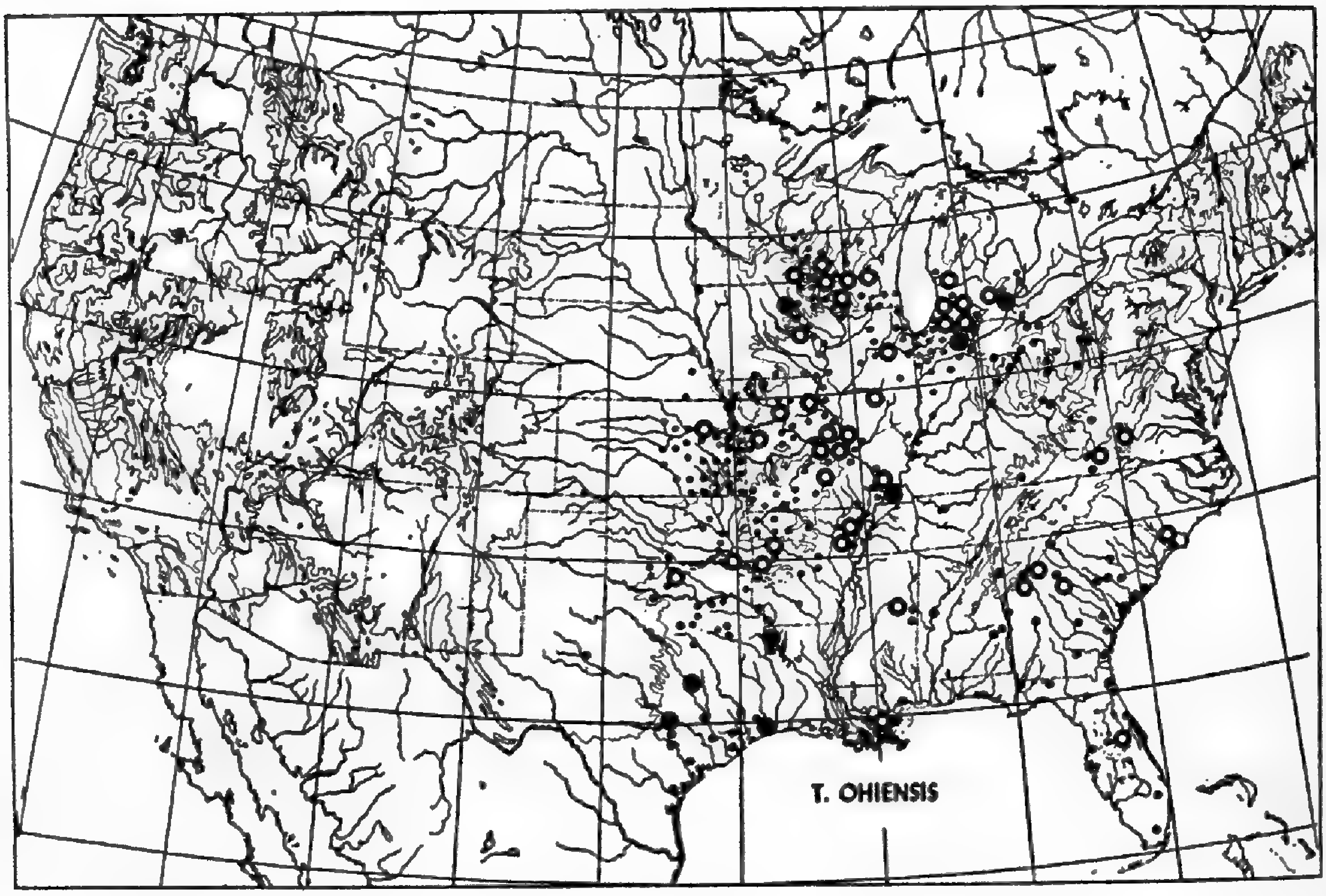
This distinctive species, characterized among other things by a velvety pubescence on the bracts, was originally native to rocky places along the front of the Edwards Plateau. It has hybridized somewhat with the other species in that area and is now spreading out actively along railroad right-of-ways, roadsides, and vacant lots. Additional collection has shown the range to extend into northern Texas. It shows marked resemblances to Mexican species which do not reach the United States. In common with *T. ohiensis* it exhibits a character of considerable phylogenetic significance in the Commelinaceae; it has multiple cymes within its large floral bracts, instead of simple cymes like most of the American species. There are counts on 70 plants from twelve localities. All were regular diploids except one plant which had an extra pair of chromosomes.



Map 9

Tradescantia ohiensis.—

This common, widespread species of the Middle West and the South has unfortunately gone by more than one name. It was referred to as *T. reflexa* in the 7th edition of Gray's *Manual* and as *T. canaliculata* in the monograph by Anderson and Woodson. *T. ohiensis* is an older name and the correct one (Fernald, 1944) according to international rules. It has a diploid area in Texas and Louisiana and another in Michigan and Indiana which has been the subject of monographic attention by Dean (1954). No irregularities were found among the diploids. Among the tetraploids three plants with extra pairs of chromosomes were found, one in Mississippi, one in Florida, and one in Arkansas. The Mississippi plant showed a marked excess of non-disjunctional divisions at meiosis; five other plants from the same locality were normal. The exceptional plant from Clarksville, Arkansas, exhibited many micronuclei which did not disjoin properly. One plant from Hamburg, Missouri, in a colony suffering extensive introgression from *T. subaspera,*

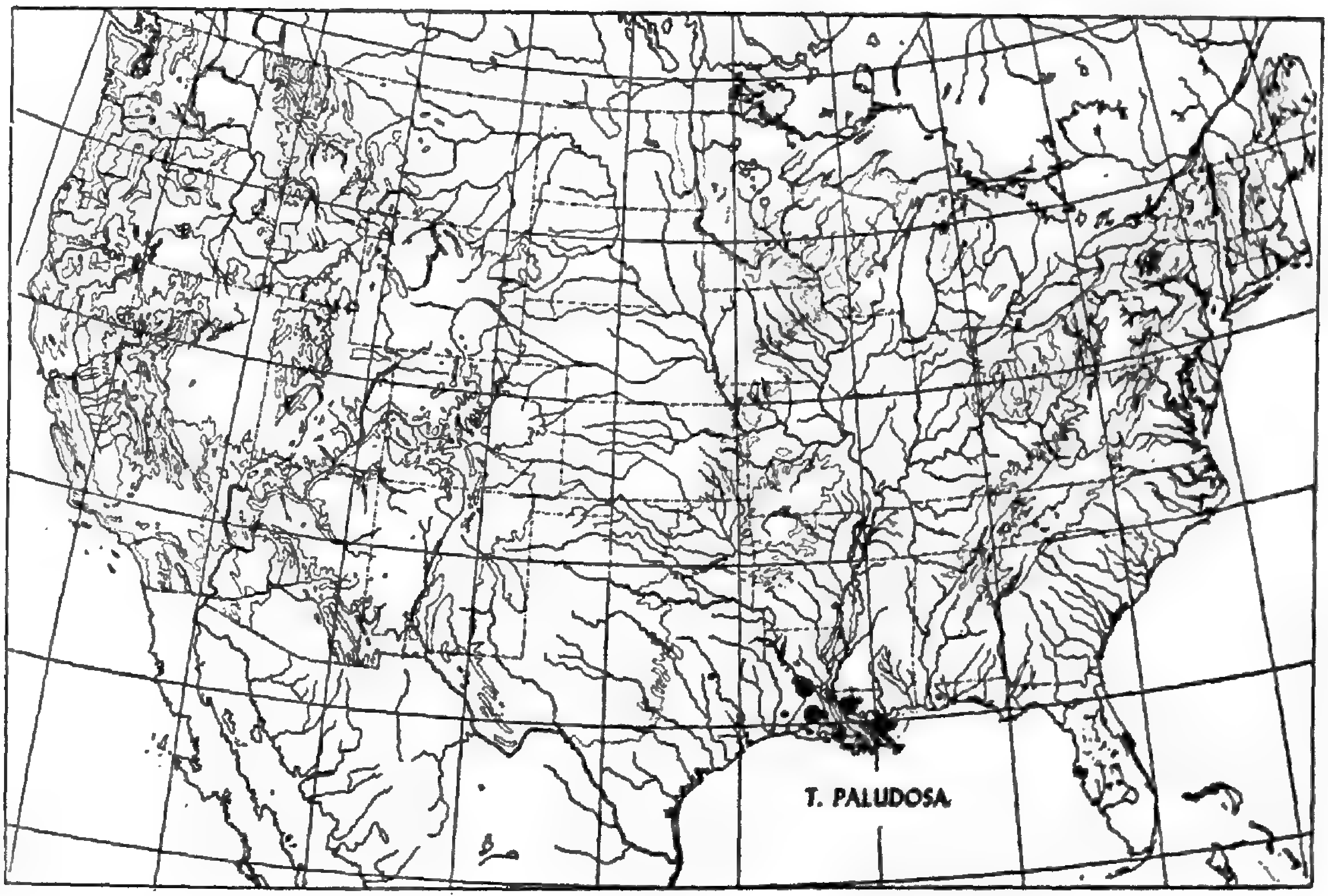


Map 10

showed many micronuclei in the microspores. One plant from Baraboo, Wisconsin, had irregular meiosis with univalents, a high percentage of non-disjunction, etc. In addition to these four plants showing irregularities of one kind or another, chromosome counts on regular tetraploids were obtained from 96 plants from 56 localities. In spite of its weedy tendencies, in spite of its auto-tetraploidy, this species for which we have a really significant sample shows only 4 per cent of obvious irregularities. All the records from the Virginia border northeastward are undoubtedly from introduced plants. The two collections from northern Michigan were apparently waifs. The species has never been re-collected in that area.

Tradescantia paludosa.—

This curious little species is native to rich Live Oak soils of the Mississippi Delta. Additional collection has extended the range of this species into southern Arkansas and eastern Texas on the same black-soil, low river-terraces from which it had previously been reported. It bears a curious morphological relationship to all the other species of the *virginiana* group. It differs very slightly from *T. ohiensis*. However, the slight differences between it and that species are all *in the direction* of the creeping tropical Tradescantias. In other words, the differences, slight as they are, would almost remove it from this group of species. It has smaller flowers, is without stomata on the upper side of its leaves, and Bramsch (1936) has shown that, unlike the other species of the *virginiana* group, it resembles the tropical Tradescantias in the large cells on the upper sides of the leaves. It also comes closer to rooting at the nodes than any other species of the *virginiana* group, close enough so that it can be rooted readily from cuttings.



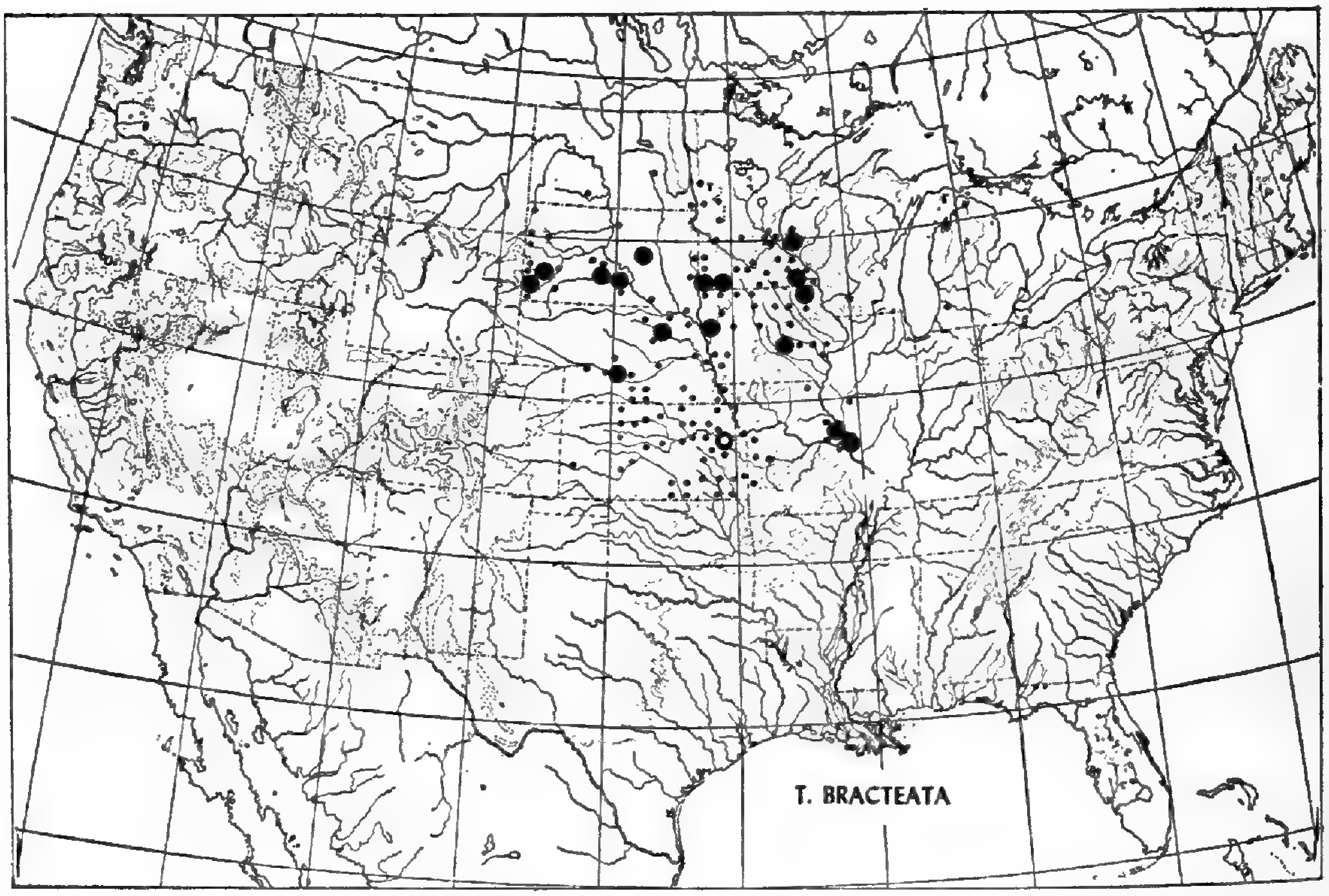
Map 11

It seems to me quite probable that *T. paludosa* originated from a rare cross between *T. ohiensis* and some tropical creeping *Tradescantia,* this hybrid backcrossing to *T. ohiensis* and producing introgressants which eventually stabilized with a very few segments (perhaps one or two chromosome arms) in what was otherwise *T. ohiensis.* The combination, however achieved, has been a boon to cytology. It combines the large, easily studied chromosomes of the *virginiana* group with the adaptability to greenhouse conditions of many tropical Tradescantias. It has become one of the standard subjects in radiation research and is one of several unexpected by-products of this investigation of chromosome-number variation.

T. paludosa is known only as a diploid. We have counts on 16 plants from four different Louisiana parishes. All these plants are regular diploids. Earlier collections were made by me from semi-domesticated plants in New Orleans gardens and from a population in the railroad yards which was hybridizing with *T. hirsutiflora* and became the object of a special investigation by Riley (1939). These were likewise diploids, but many plants among them had tiny fragment chromosomes, sometimes in very large numbers. These fragments have been the object of special investigations by Whitaker and others (Whitaker, 1939).

Tradescantia bracteata.—

The peculiar binary variation pattern of this species has been the object of a special investigation (Anderson and Hubricht, 1938). The species is a diploid. Chromosome numbers were determined of 40 plants from 25 localities. Two plants from Lawrence, Kansas, were tetraploids and two from Grinnell, Iowa, were triploids; all the rest were regular diploids. I have suggested (Anderson and Hubricht, 1938) that under the prairie and plains conditions where this species is native, ploidy, with its tendency to increase length of blooming season, would be at a selective disadvantage. The plants from Grinnell and Lawrence show that polyploid strains can arise in this species. The Michigan collection has been checked and represents a truly disjunct distribution, something which is rather rare in these Tradescantias. The record from Indiana in Anderson and Woodson was a depauperate specimen of *T. virginiana*.



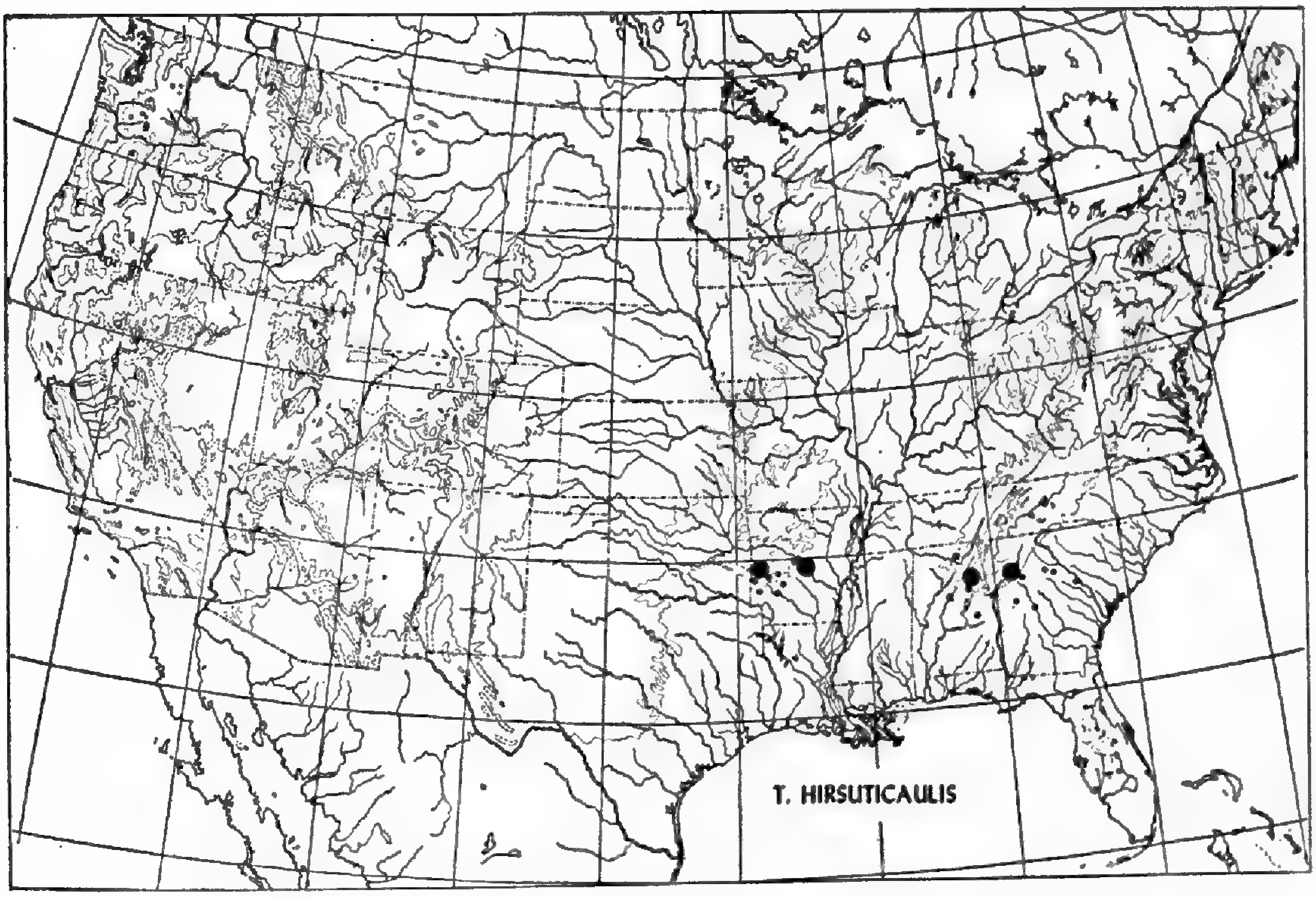
Map 12

Tradescantia hirsuticaulis.—

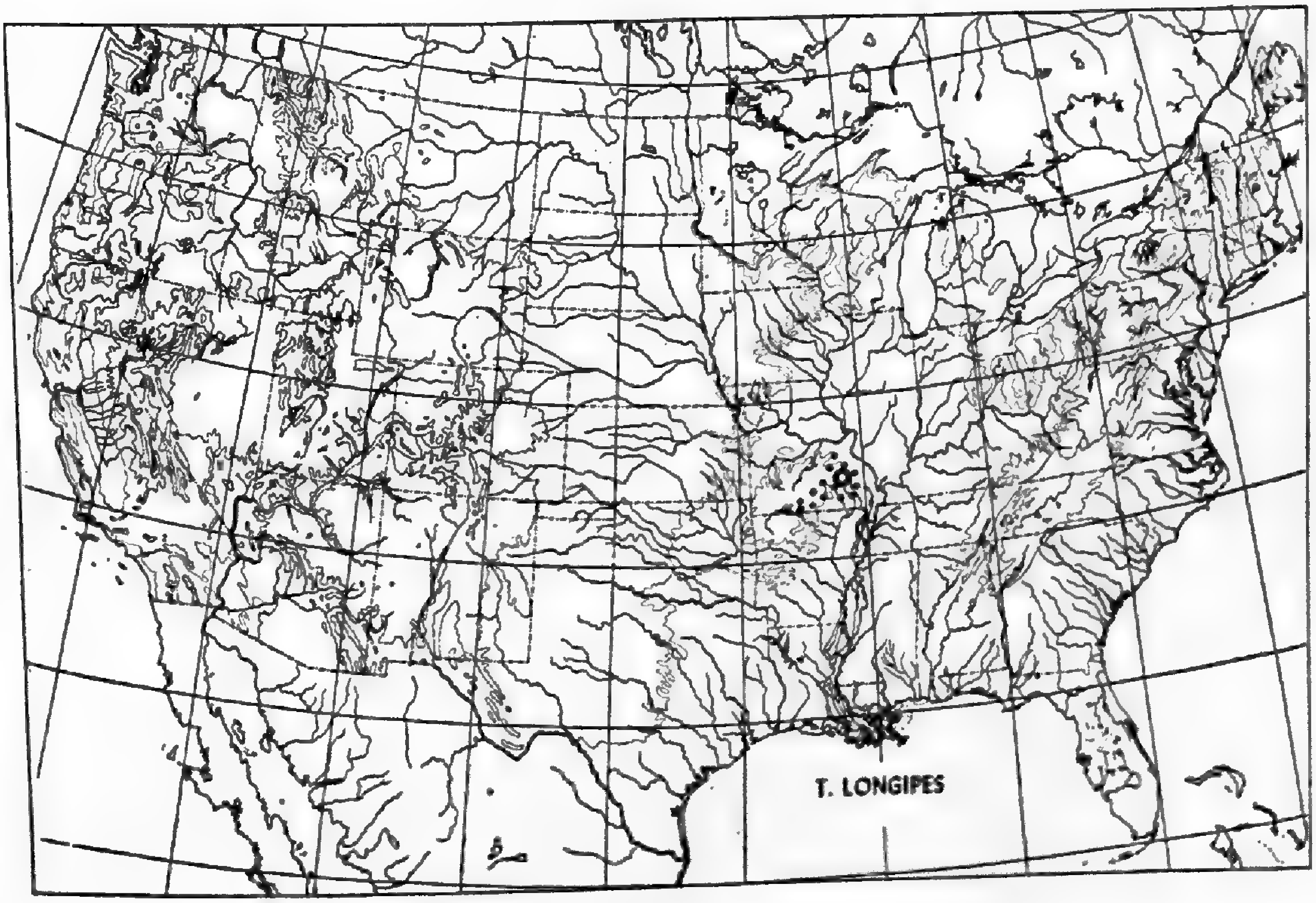
This species is exclusively diploid. Twenty-one plants were examined from ten localities. At two localities plants were found with an extra pair of chromosomes. There were also chromosome fragments in these two plants. One plant from still another locality had very small fragment chromosomes in addition to the diploid complement. These three abnormal plants were from Stone Mountain, Georgia, eastern Arkansas and western Arkansas.

Tradescantia longipes.—

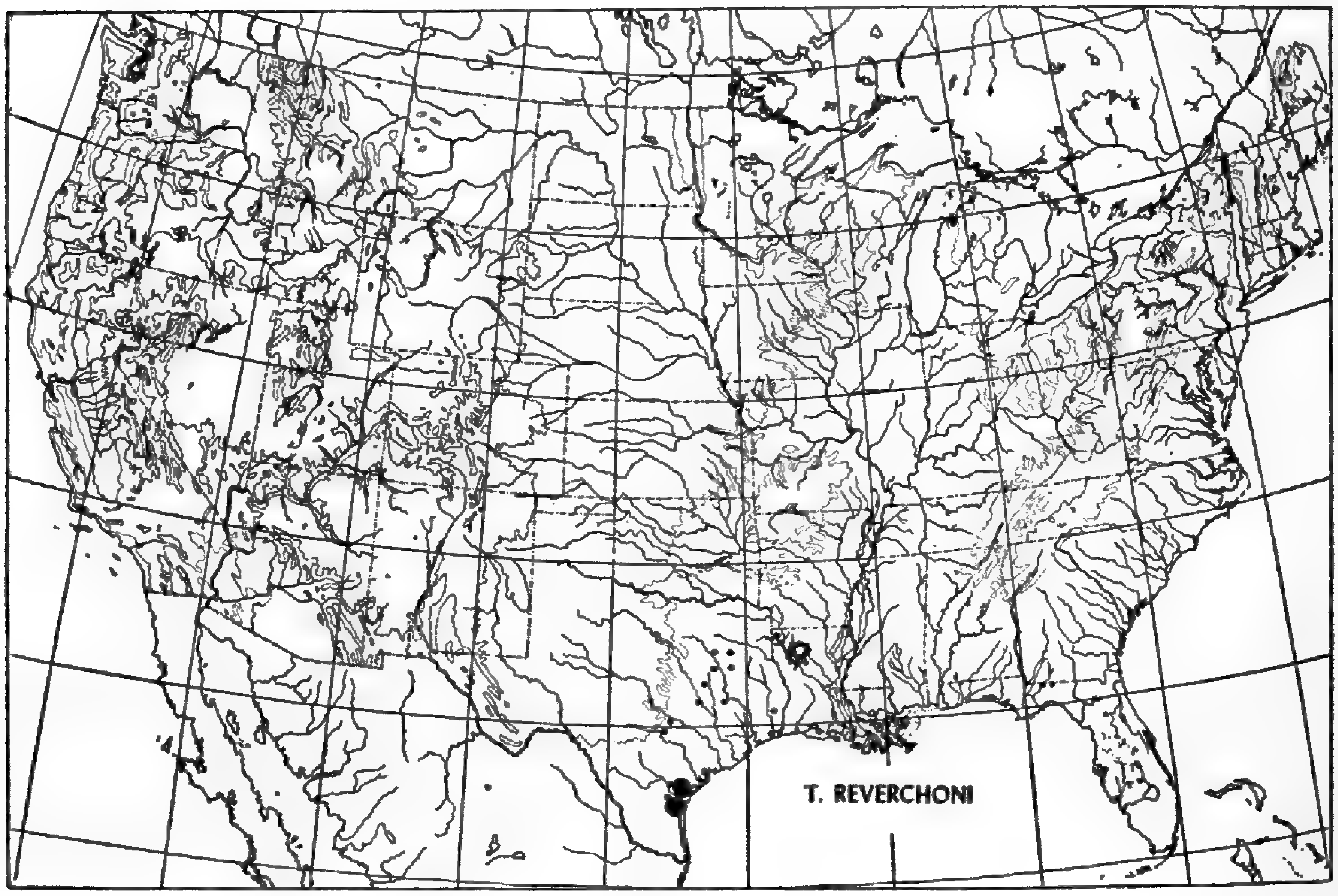
I have three counts on this species from three different localities in Missouri. All three were regular tetraploids. Further collecting has extended the distribution to St. James County, Missouri, on the same general type of soil.



Map 13



Map 14



Map 15

Tradescantia reverchoni.—

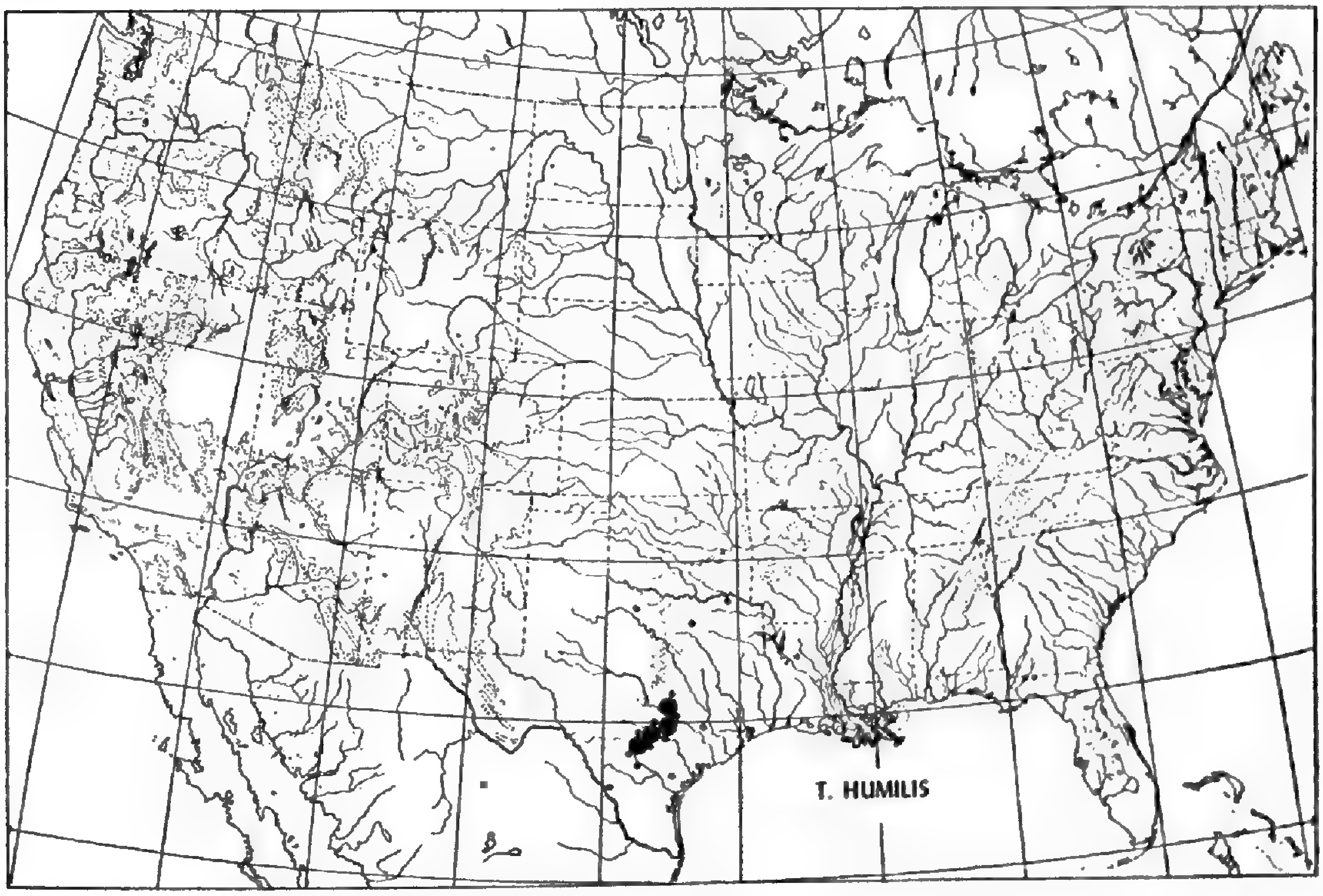
This species is found along the Carizo sand ridge in Texas and on coastal sands. When these sandy soils are brought under cultivation for truck crops, as near Winter Haven, Texas, *T. reverchoni* may hybridize extensively with *T. occidentalis.* We have counts on five plants from two localities in Texas; all were regular diploids. One plant was counted in northwestern Louisiana; it was a regular tetraploid.

Tradescantia humilis.—

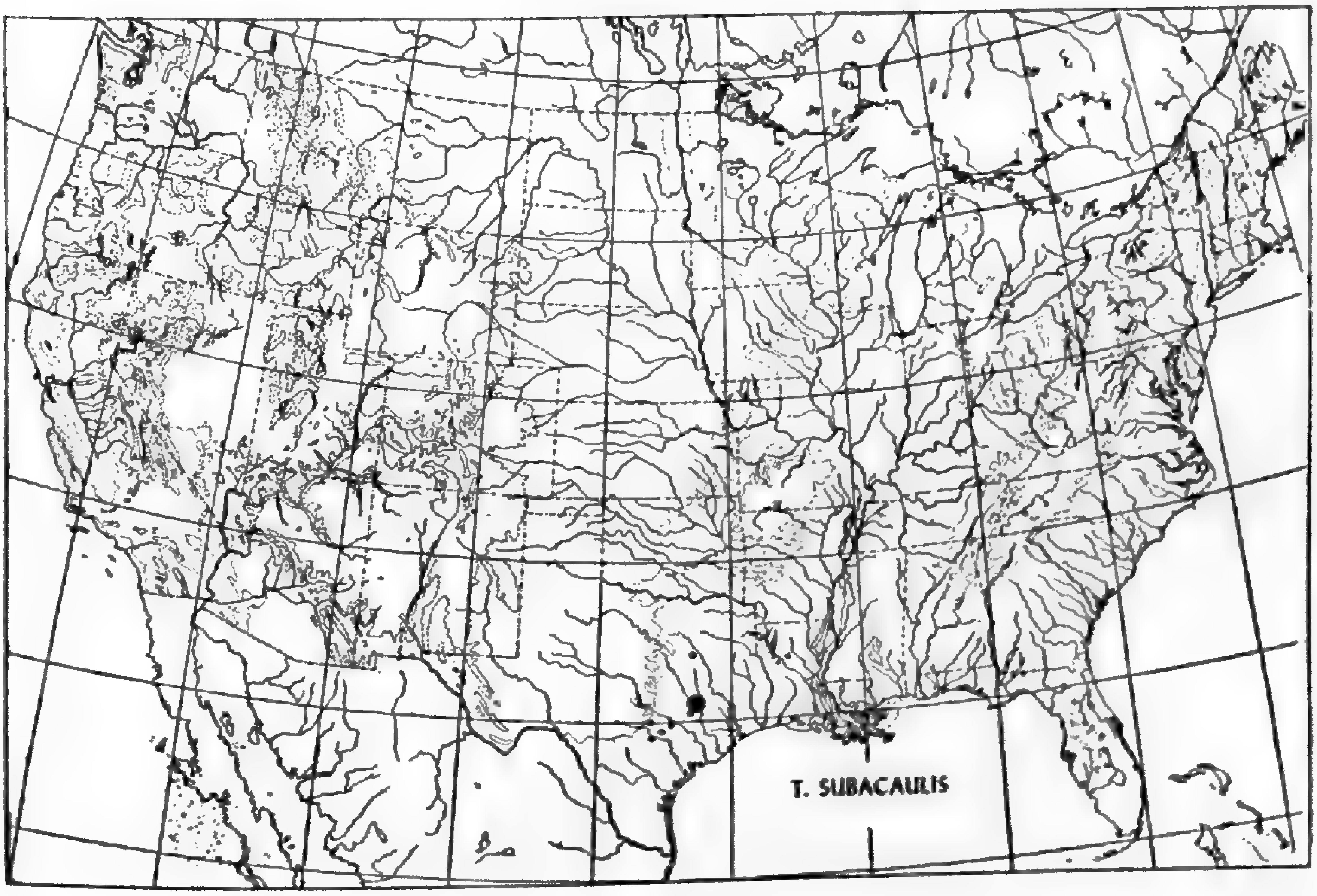
This species was native to the rich black soil at the edge of the coastal plain in Texas and was so common and so conspicuous as to have been collected frequently by early naturalists. Virtually all this land is now in cultivation (much of it in cotton) or in cities and military camps. *T. humilis* lingers on around the fringes of its former home. I have found it along railroads, in bee yards, along roadsides, behind sign boards, in real-estate developments, and along the fences around military establishments. Most of the specimens I collected showed signs of slight introgression from other species, as might be expected under such conditions. Sixteen plants were counted in seven localities; all were regular diploids.

Tradescantia subacaulis.—

This species was counted in two localities. Both plants were regular diploids. While I knew the species well in the herbarium I had not seen it in the field until I made these two collections. It comes up in deep sand, and much of the stem is subterranean. The plant is also rather more succulent than the other species in the *virginiana* group. When it is dug up out of the sand and dried out in a plant



Map 16

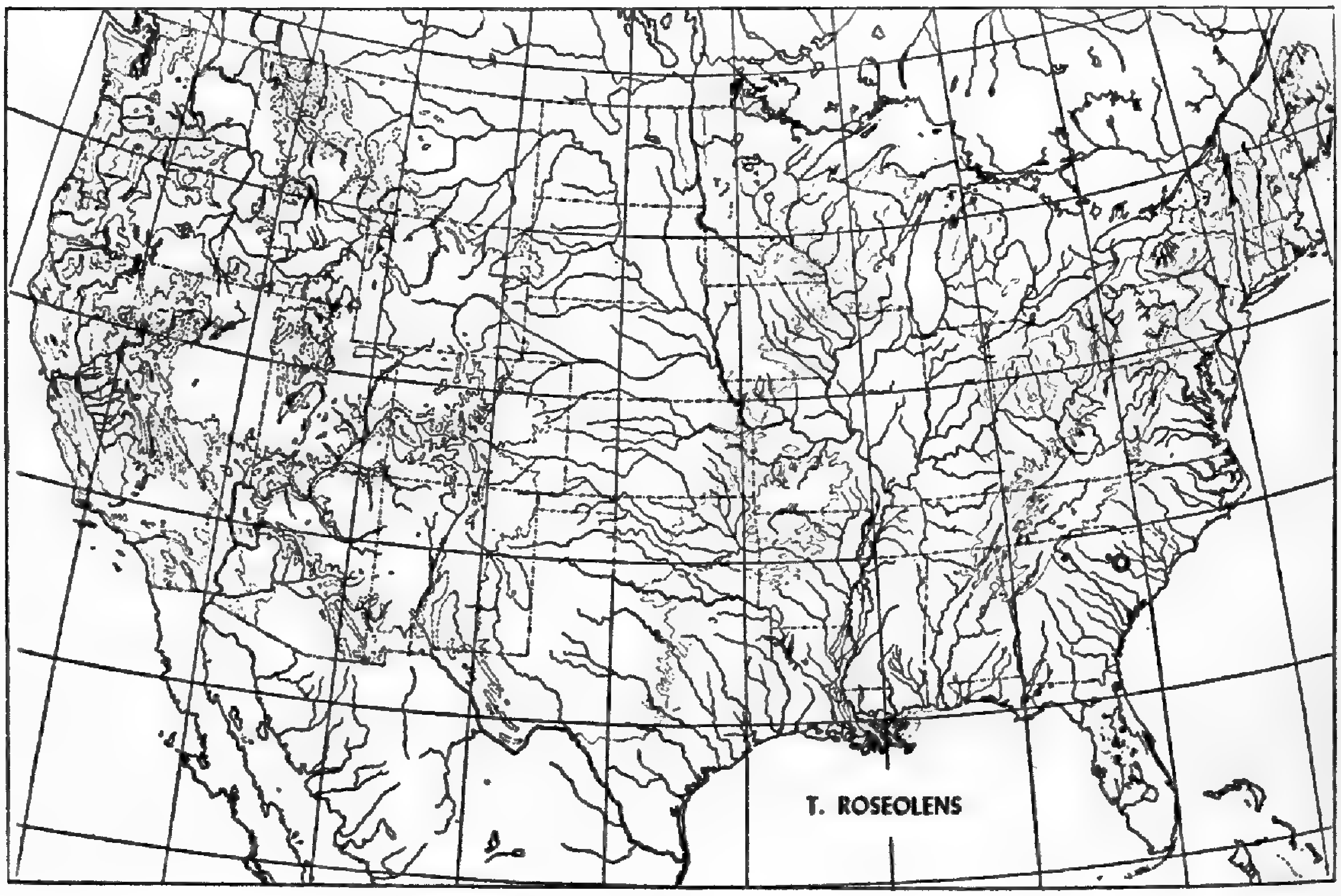


Map 17

press it changes its aspect more radically than any of our other *Tradescantias*. It was therefore not until my specimens were nearly dry that I realized I had at last found *T. subacaulis.*

Tradescantia roseolens.—

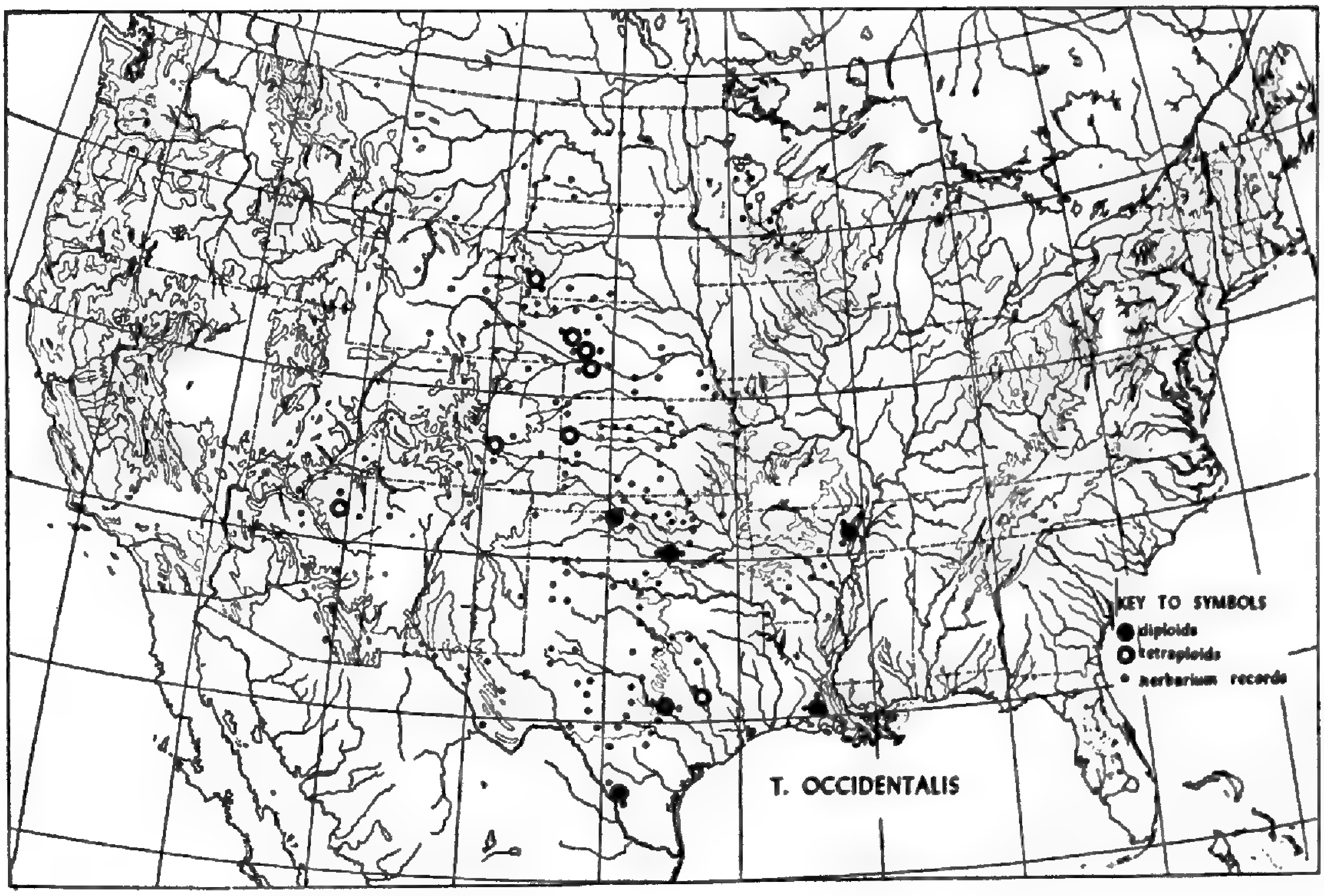
This species was found in the field only once. Five plants were counted; all were regular tetraploids.



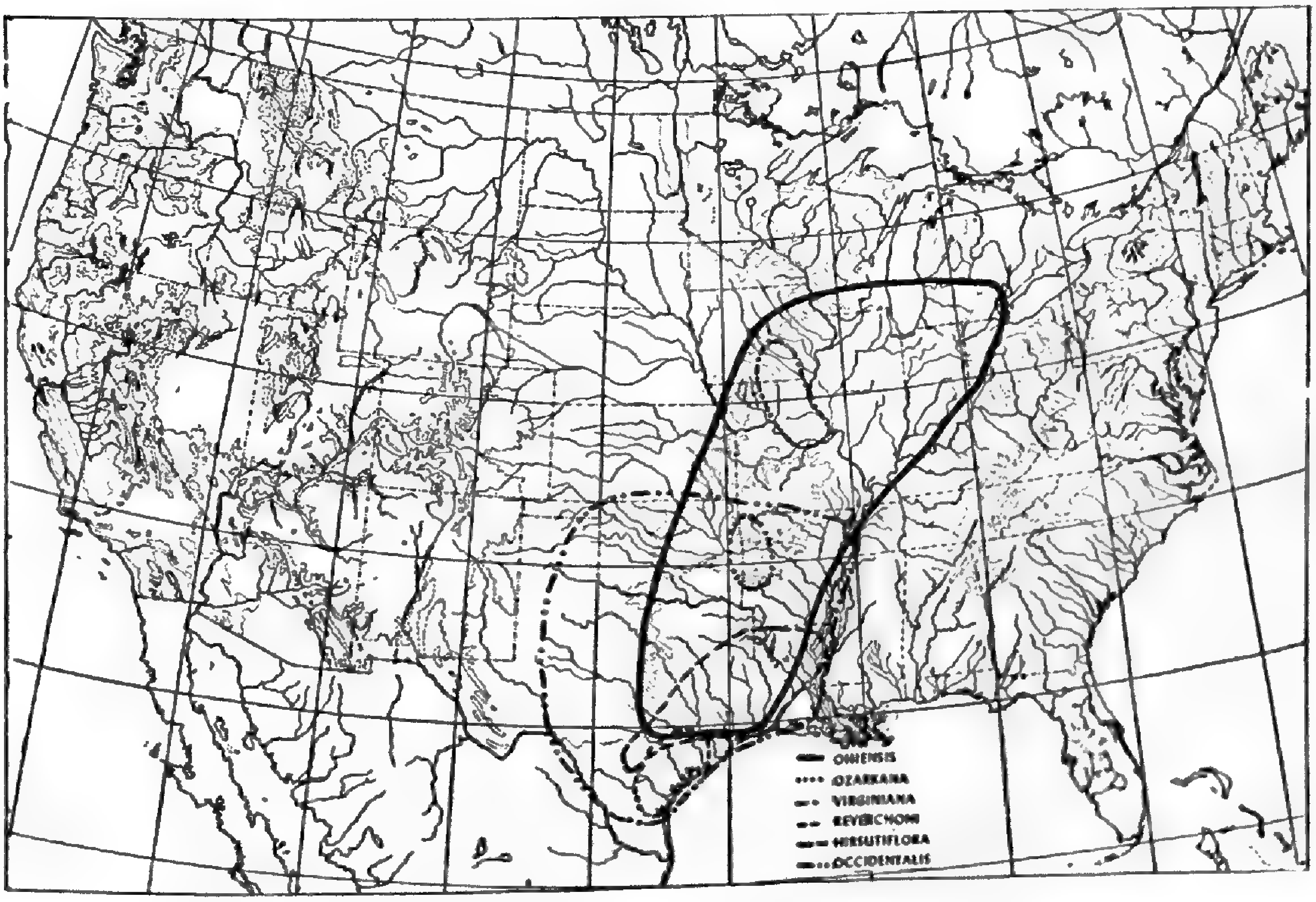
Map 18

Tradescantia occidentalis.—

This species is differentiated both geographically and ecologically. Out of it is coming one of the most aggressive weeds in the Great Plains. Further collecting has extended the record of this species in Louisiana and Arkansas where it is a common plant on sandy terraces which supported natural prairies before they were brought into cultivation. In parts of Texas one can find slender diploid plants of *T. occidentalis* in among the mesquite bushes and coarse tetraploids of *T. occidentalis* along the highway a few feet away. On many a remote mesa in the Great Plains, however, there will be slender little plants, far from any highway, which are tetraploids. Furthermore, the weedy strains are themselves demonstrably differentiated geographically. Part of this, it has been demonstrated elsewhere (Anderson and Hubricht, 1938), is due to extensive introgression from *T. ohiensis* which is actively spreading westward far beyond the range of *T. ohiensis* itself. Forty chromosome counts were made at 22 localities. At seven localities the 11 plants counted were regular diploids. At 15 localities the 29 plants counted were tetraploids. One of these plants was somewhat irregular with many univalents, and with micronuclei in the microspore. The other 28 were regular.



Map 19



Map 20

Diploid areas of species which are elsewhere tetraploid. It will be noted that these areas tend to center upon Texas as do most of the purely diploid species.

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Plant Name Anderson & Sax (1936)	Locality	2n	4n	2n +2	4n +2
T. subaspera var. *typica*					
	Florida, Torreya State Park		2		
Mordock	Illinois, north of Valmeyer, Monroe Co.		1		
Hazleton	Indiana, Hazleton		1		
New Harmony	Indiana, New Harmony, Posey Co.		1		
Turkey Run	Indiana, Turkey Run		3		
Louisville	Kentucky, Louisville		1		
Smith's Mill	Kentucky, Smith's Mill		1		
Ashland	Missouri, Ashland, Boone Co.		1		
Fertile	Missouri, Fertile, Washington Co.		1		
Hermann	Missouri, Hermann		1		
Marthasville	Missouri, Marthasville		3		
Wolf Creek	Tennessee, near Wolf Creek	1			
T. subaspera var. *montana*					
Anniston	Alabama, Anniston		1		
Gravel Pit	Alabama, Jacksonville		3		
Hair	Alabama, Jacksonville		3		
Balsam Gap	North Carolina, Balsam Gap		8		1
Cherokee	North Carolina, Cherokee		1		
Mt. Mitchell	North Carolina, Mt. Mitchell		5		
Sylva	North Carolina, Sylva		1		
Knoxville	Tennessee, Knoxville		2		
T. edwardsiana					
Edwardsiana	Texas, near Austin	15			
Bull Creek	Texas, Bull Creek	2			
T. ozarkana					
	Arkansas, Deer		1		
Boston Mtns.	Arkansas, south of Jasper, Newton Co.		1		
Heinze	Arkansas, Rich Mountain, Polk Co.	1			
Hotel	Arkansas, Rich Mountain, Polk Co.	3			
Roaring River	Missouri, Roaring River State Park, Barry Co.		1		

Plant Name Anderson & Sax (1936)	Locality	2n	4n	2n +2	4n +2
T. ernestiana					
	Arkansas, Rich Mountain, Polk Co.	1			
Eagle Rock	Missouri, Eagle Rock, Barry Co.	1			
Jasper	Missouri, Jasper Co.	1			
Elk River	Missouri, Noel, McDonald Co.	2			
Julian	Missouri, Richville, Douglas Co.	4			
T. virginiana					
New Athens	Illinois, 1 mi. west of New Athens, St. Clair Co.	3			
Tobacco Landing	Indiana, Harrison Co.		1		
Portland	Indiana, Portland		1		
H.S.C.	Iowa, Skunk River, Poweshiek Co.	3			
Skunk River	Iowa, bluffs along N. Skunk River, north of Sharon, Poweshiek Co.	2			
Algovirg	Missouri, Algonquin Sta., Webster Groves, St. Louis Co.		1		
Fowler Creek	Missouri, east of Ashland, Boone Co.	1			
DeSoto	Missouri, DeSoto, Jefferson Co.				1
Dry Fork	Missouri, Dry Fork	1			
	Missouri, 7 mi. south of Fredericktown, Madison Co.		2		
	Missouri, Goldman, Jefferson Co.		2		
	Missouri, ½ mi. east of Greenville, Wayne Co.		3		
Koester	Missouri, Koester, St. Francois Co.		1		
New Florence	Missouri, New Florence, Montgomery Co.	1			
New Melle	Missouri, New Melle, St. Charles Co.	1			
Mineola	Missouri, Mineola	1			
Cherbonnier	Missouri, 5 mi. west of St. Charles	1			
Selma	Missouri, Selma, Jefferson Co.		1		
Mattese	Missouri, Mattese, St. Louis Co.		1		
Vera	Missouri, Vera, Pike Co.	4			
Peterson	Missouri, Warrenton	1			
Swarthmore	Pennsylvania, Swarthmore		2		
Fort Valley	Virginia, Fort Valley		1		
T. hirsutiflora					
	Arkansas, northeast of Little Rock, Pulaski Co.		1		
Perry	Georgia, Athens		1		
Dorsut	Louisiana, Caddo Parish	1		1	
	Louisiana, Iowa	5			
	Louisiana, L.S.U., Natchitoches, Natchitoches Parish		1		
	Louisiana, Mooringsport Road, Shreveport	2			
	Louisiana, between Scott and Duson		2		
	Texas, west of China	1			
	Texas, 14 mi. south of College Station, Brazos Co.	2			
Corer Lane	Texas, Corer Lane, Wilson Co.	2			
	Texas, between Fairbanks and Cypress	1		1	
	Texas, Gutz Clay Pit Road	1			
Flory	Texas, Hearne, Robertson Co.	1			
Ledbetter	Texas, 1 mi. east of Ledbetter, Fayette Co.	1			
	Texas, east of Liberty	1			
Sutherland Springs	Texas, Sutherland Springs	2			
T. tharpii					
	Kansas, Miltonvale, Cloud Co.		1		
Rocky Prairie	Missouri, Webb City, Jasper Co.		1		
Scullin	Oklahoma, Scullin		5		

Plant Name Anderson & Sax (1936)	Locality	2n	4n	2n +2	4n +2
T. gigantea					
Cliff Springs	Texas, Austin	18			
Lake Cliff	Texas, Austin	1			
Mo. Pac.	Texas, Austin	8		1	
Onion Creek	Texas, Austin	7			
River Cliff	Texas, Austin	2			
River Terrace	Texas, Austin	5			
Shoal Creek	Texas, Austin	7			
Terrace	Texas, Austin	12			
Bear Mtn.	Texas, Bear Mountain, Gillespie Co.	2			
Buda	Texas, Buda	1			
	Texas, bank of Guadalupe River, Gruene, Comal Co.	1			
Hunter	Texas, Hunter	1			
Mt. Bonnell	Texas, Mt. Bonnell	5			
T. ohiensis					
	Arkansas, Kings Canyon, Clarksville		5		1
	Arkansas, Y-City, Scott Co.		1		
Orlando	Florida, Orlando		1		1
Borglum	Georgia, Stone Mountain		1		
Warrenton	Georgia, Warrenton		1		
Warrenton	Georgia, Warrenton		1		
	Illinois, Bellflower, McLean Co.		2		
Pana	Illinois, Pana		1		
	Illinois, Roberts, Ford Co.		2		
Starved Rock	Illinois, Starved Rock, LaSalle Co.		1		
Ullin	Illinois, Ullin		1		
Diamond Lake	Indiana, Diamond Lake, Noble Co.	2			
	Indiana, Indiana Dune State Park		4		
Waterloo	Iowa, Waterloo	1			
	Kansas, Belvue, Pottawatomie Co.		5		
	Kansas, Belvue		2		
	Kentucky, Bardwell	1			
Dorcan	Louisiana, Caddo Parish	1			
	Louisiana, near Saline		2		
	Louisiana, near Shreveport	1			
Steere	Michigan, Ann Arbor	2			
	Michigan, Cedar Springs, Kent Co.		1		
	Michigan, Dexter	5			
Dexter	Michigan, Dexter	1			
Old Mill	Michigan, Grass Lake, Jackson Co.		1		
	Michigan, Homer, Calhoun Co.		1		
	Michigan, Litchfield, Hillsdale Co.		1		
Schoolcraft	Michigan, Portage, Kalamazoo Co.		1		
Reita	Michigan, Schoolcraft		1		
3 Rivers	Michigan, Three Rivers		1		
	Minnesota, Peterson		1		
McKee	Mississippi, State College		6		1
Algonquin	Missouri, Algonquin Sta., Webster Groves, St. Louis Co.		6		
Antonia	Missouri, Antonia, Jefferson Co.		2		
	Missouri, east of Brookfield, Linn Co.		1		
	Missouri, 5 mi. north of Drake, Gasconade Co.		1		
Florissant	Missouri, Florissant, St. Louis Co.		1		
Hamburg	Missouri, Hamburg		4		
La Barque	Missouri, La Barque Creek		1		
Red Rock	Missouri, Red Rock, Hughes Mountain		1		
Royal Gorge	Missouri, Royal Gorge, Iron Co.		1		

Plant Name Anderson & Sax (1936)	Locality	2n	4n	2n +2	4n +2
Wash. U.	Missouri, St. Louis		2		
Berry	Missouri, Warrensburg, Johnson Co.		2		
South Webster	Missouri, Webster Groves, St. Louis Co.		1		
Bolton	North Carolina, Bolton		3		
	Oklahoma, Hughes		1		
Platt Nat. Park	Oklahoma, Platt National Park, Murray Co.		1		
Turner Falls	Oklahoma, Turner Falls, Murray Co.		1		
Reflexa	Texas, Austin	1			
	Texas, Hearne	1			
Keller	Texas, Keller	2			
	Texas, between Pine Island and China	2			
	Virginia, Eagle Rock		1		
Mountain Lake	Virginia, Mountain Lake, Giles Co.		1		
Madison	Wisconsin, Arena		1		
Baraboo	Wisconsin, Baraboo		2		
	Wisconsin, 6 mi. northwest of Baraboo, Sauk Co.		2		
	Wisconsin, 3 mi. northwest of Big Spring, Adams Co.		1		
	Wisconsin, 2 mi. southwest of Caloma, Waushara Co.		1		
	Wisconsin, 3 mi. east of Friendship, Adams Co.		2		
Jollivette	Wisconsin, La Crosse		2		
	Wisconsin, Nekoosa, southeast corner Wood Co.		1		
	Wisconsin, Plainfield Lake, Waushara Co.		2		
	Wisconsin, Spring Green		1		
Tomah	Wisconsin, Tomah		1		
	Wisconsin, Viroqua		1		
	Wisconsin, 3 mi. south of Wisconsin Dells, Adams Co.		2		
	Wisconsin, 9 mi. north of Wisconsin Dells, Adams Co.		2		
T. paludosa					
Acadosa	Louisiana, Acadia Parish	1			
Brown	Louisiana, Baton Rouge	1			
	Louisiana, Bennettsville, Rapides Parish	1			
Gentilly	Louisiana, Gentilly	13			
T. bracteata					
Clarke	Iowa, Grinnell	1			
Grinnell	Iowa, Grinnell	2			
Harriss Grove	Iowa, 4 mi. north of Grinnell, Poweshiek Co.	2			
Kellogg	Iowa, Kellogg, Jasper Co.	1			
Kendallville	Iowa, Kendallville, Winneshiek Co.	1			
Pierson	Iowa, Pierson, Woodbury Co.	1			
Tama	Iowa, Tama	3			
Victor	Iowa, 1 mi. west of Victor, Poweshiek Co.	1			
	Kansas, Lawrence		2		
Gates	Kansas, Manhattan	2			
Manhattan	Kansas, Manhattan	1			
Rock	Minnesota, Beaver Creek, Rock Co.	1			
Preston	Minnesota, Preston, Fillmore Co.	1			
Worthington	Minnesota, Worthington	1			
Chain of Rocks	Missouri, Chain of Rocks, St. Louis Co.	1			
Portage des Sioux	Missouri, Portage des Sioux, St. Charles Co.	8			
Overton	Nebraska, Overton, Dawson Co.	3			
Royal	Nebraska, Royal	1			
Huron	South Dakota, Huron, Beadle Co.	1			
Kennebec	South Dakota, Kennebec	1			
Murdo	South Dakota, Murdo	1			
Rockerville	South Dakota, Rockerville, Pennington Co.	1			
Wasta	South Dakota, Wasta, Pennington Co.	2			
S. Dakota	South Dakota, Wind Cave, Custer Co.	1			
Houlton	Wisconsin, Houlton, St. Croix Co.	1			

Plant Name Anderson & Sax (1936)	Locality	2n	4n	2n +2	4n +2
T. hirsuticaulis					
Jacksonville	Alabama, Jacksonville	2			
Showal	Alabama, Jacksonville	1			
Quad Petal	Alabama, Whites Gap	1			
Whites Gap	Alabama, Whites Gap	1			
	Arkansas, northeast of Little Rock, Pulaski Co.	5			
Montgomery	Arkansas, Montgomery Co.	6			
Y-City	Arkansas, Y-City, Scott Co.	2		1	
North Slope	Georgia, Stone Mountain	1		1	
T. longipes					
Killarney	Missouri, Lake Killarney, Iron Co.		1		
	Missouri, Old Silver Mine, Madison Co.		1		
Spring Creek	Missouri, 5 mi. north of Stanton, Franklin Co.		1		
T. reverchoni					
Lucky	Louisiana, Lucky, Bienville Parish		1		
Flour Bluff	Texas, Flour Bluff	1			
	Texas, Ingleside, near Corpus Christi	4			
T. humilis					
Nigger D. & D.	Texas, Austin	3			
	Texas, Lockhart, Caldwell Co.	1			
	Texas, New Braunfels, Comal Co.	2			
	Texas, 10 mi. south of New Braunfels, Comal Co.	1			
Oakhill	Texas, Oakhill Road	7			
	Texas, Saline	1			
	Texas, W. W. White Road, Kyle	1			
T. subacaulis					
	Texas, Bryan, Brazos Co.	1			
	Texas, south of College Station, Brazos Co.	1			
T. roseolens					
Columbia	South Carolina, Columbia		5		
T. occidentalis					
Winslow	Arizona, Winslow		1		
Ellsmere	Colorado, Ellsmere		1		
Manitou	Colorado, Manitou		1		
Somena	Kansas, Somena		1		
	Louisiana, between Scott and Duson	2			
Brady	Nebraska, Brady, Lincoln Co.		1		
Chadron	Nebraska, Chadron, Dawes Co.		1		
Tryon	Nebraska, Tryon		1		
	Nebraska, Tryon, McPherson Co.		1		
	Nebraska, Whitman, Grant Co.		2		
Belew	Oklahoma, Harmon	1			
	Oklahoma, Indian Springs, south of Norman	1			
Paoli	Oklahoma, Paoli	1			
Horsethief Lake	South Dakota, Horsethief Lake		1		
S. Dakota	South Dakota, Wind Cave, Black Hills		1		
Austin	Texas, Austin	4			
Ilex Grove	Texas, College Station		8		
Jeanette	Texas, College Station		3		
Mangelsdorf	Texas, College Station		4		
Signal	Texas, College Station		2		
	Texas, 14 mi. south of College Station	1			
	Texas, Miranda, Webb Co.	1			

Species of *Tradescantia*	2n		4n		2n + 2		4n + 2	
	Populations	Individuals examined	Populations	Individuals examined	Populations	Individuals examined	Populations	Individuals examined
subaspera typica	1	1	11	16	....	....	....	....
subaspera montana	....	....	8	24	....	....	1	1
edwardsiana	2	17	....	....	....	....	....	....
ozarkana	2	4	3	3	....	....	....	....
ernestiana	5	9	....	....	....	....	....	....
virginiana	11	19	11	16	....	....	1	1
hirsutiflora	12	20	4	5	2	2	....	....
tharpii	....	....	3	7	....	....	....	....
gigantea	13	70	....	....	1	1	....	....
ohiensis	12	20	56	96	....	....	3	3
paludosa	4	16	....	....	....	....	....	....
bracteata	24	39	1	2	....	....	....	....
hirsuticaulis	8	19	....	....	2	2	....	....
longipes	....	....	3	3	....	....	....	....
reverchoni	2	5	1	1	....	....	....	....
humilis	7	16	....	....	....	....	....	....
subacaulis	2	2	....	....	....	....	....	....
roseolens	....	....	1	5	....	....	....	....
occidentalis	7	11	15	29	....	....	....	....
	112	268	117	207	5	5	5	5

Total populations studied	230
Total individuals examined	485

INTROGRESSION OF *SALVIA APIANA* AND *SALVIA MELLIFERA*

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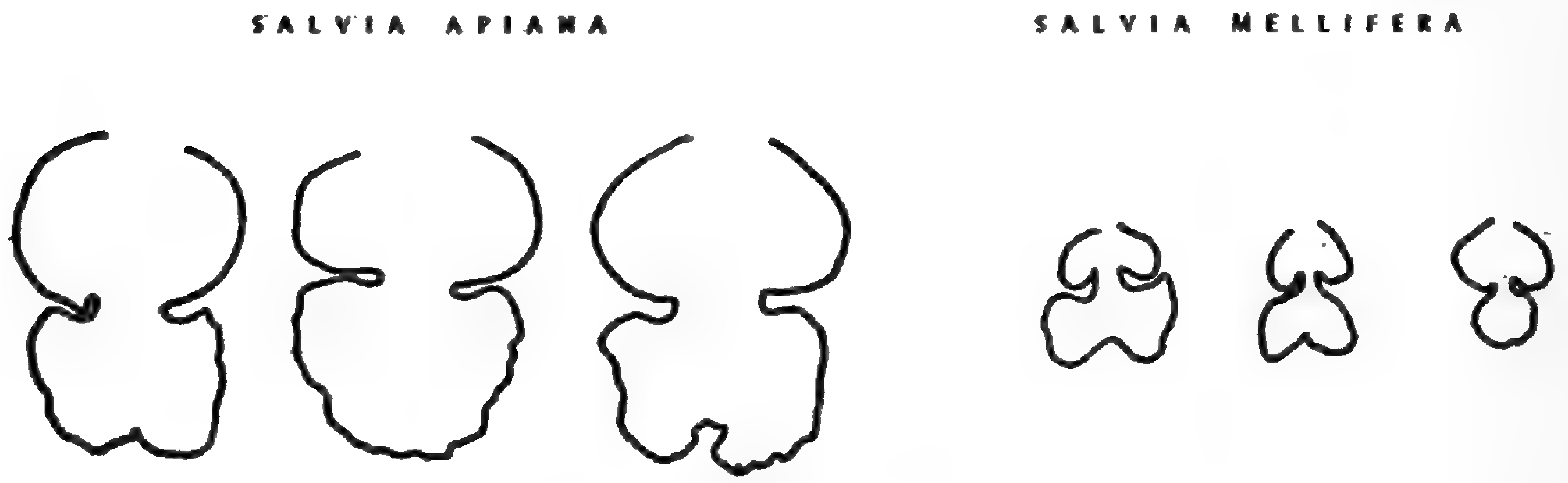
Salvia apiana and *Salvia mellifera* are two common species of sage in coastal California. Over much of their overlapping ranges they give little or no indication that they can (and frequently do) hybridize and that their hybrids are quite fertile. These significant facts were called to scientific attention by Epling. After monographing these and other Salvias taxonomically (Epling, 1938), he studied them experimentally in the field and in the breeding plot. He demonstrated (Epling, 1947) that they hybridize readily when artificially cross-pollinated and that the resulting hybrids are fertile enough to yield variable F-2's and back-crosses. Though these two species grow closely intermingled over thousands of square miles he found little evidence that hybridization did take place except under disturbed conditions. This he interpreted as due to a complex of internal and external barriers. One of the most important is the different adaptive mechanisms for insect pollination in the two species, S. *apiana* being pollinated largely by bumble bees and S. *mellifera* by small solitary bees.

The problem seemed such an interesting one that the senior author has studied it repeatedly and intensively in the field for somewhat over a decade and has used these two species as field and laboratory material for a summer school course. Population samples from critical areas were pickled for laboratory study, and with the help of the junior author an exhaustive analysis of variation in pubescence, calyx shape, corolla shape, and inflorescence branching was undertaken. This confirms and extends Epling's experimental and field studies. It analyzes a little more precisely the conditions under which the barriers break down between the two species. Thanks are due to Carl Epling, to Harlan Lewis, and to E. G. Anderson for assistance in making the collections.

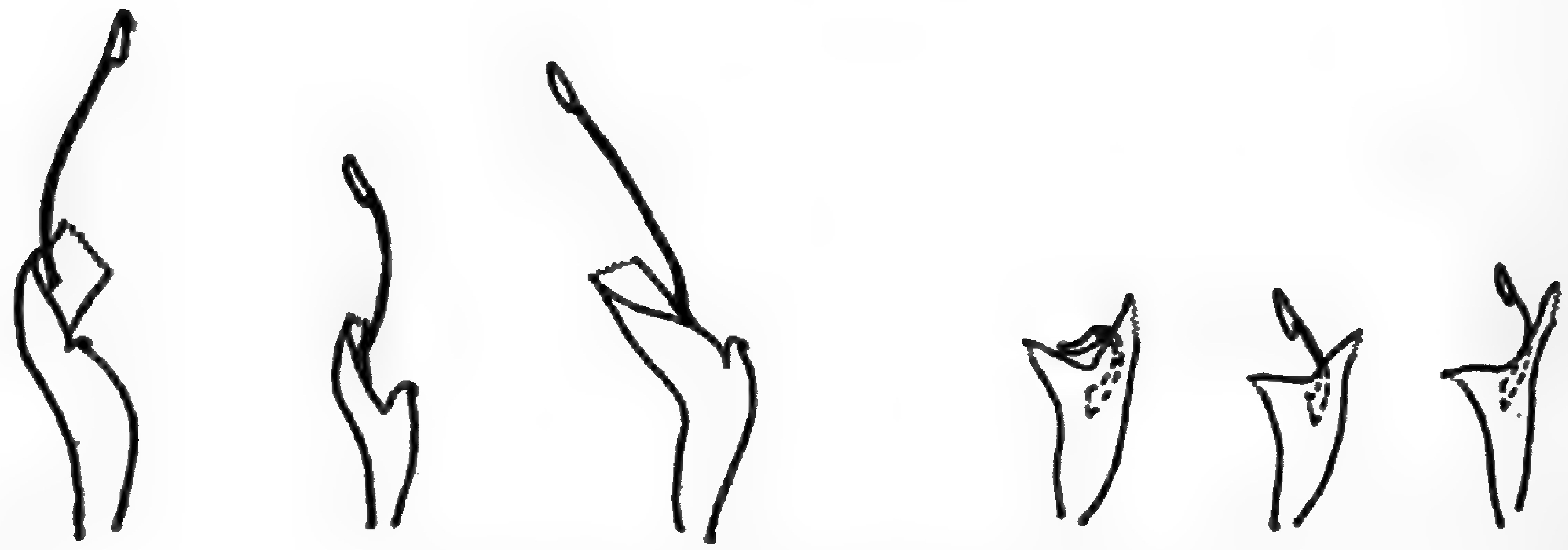
In addition to the various facts collected by Epling, careful study of two quite different matters seemed necessary before we could interpret the hybridization dynamics of these two species: (1) a more complete morphological analysis of the two species and their intermediates; (2) a precise investigation of the disturbed habitats in which intermediates were common.

MORPHOLOGICAL ANALYSIS OF SPECIES DIFFERENCES

If one is effectively to analyze the variation pattern in populations where hybridization is known or suspected, the first *desideratum* is a thorough understanding of the nature of the differences between the hybridizing entities. *Salvia apiana* and *Salvia mellifera* are well-differentiated species, distinguishable at a glance, but if we are to use this difference as a yardstick in measuring what is happening in populations, we must refine our understanding of it to the point where we can distinguish S. *mellifera* with eight ancestors out of eight belonging to

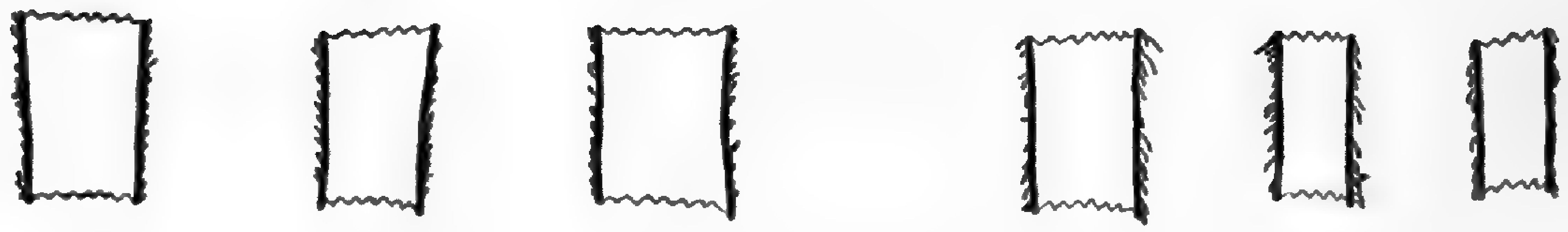


Lower lip of corolla.



Corolla tube showing insertion of stamens and filament length

Calyx



Axis of inflorescence

Fig. 1. Drawings of portions of *Salvia* flowers used in analyzing variation pattern. Comparable portions of three plants of *Salvia apiana* and three of *Salvia mellifera* were drawn to scale with camera lucida. Upper row (× 2); second row (× 2) showing filament lengths and position of stamen insertion in corolla tube; third row, calyx × 2), showing length of terminal spine and length of pubescence; bottom row (× 8), view from the side showing length and direction of pubescence.

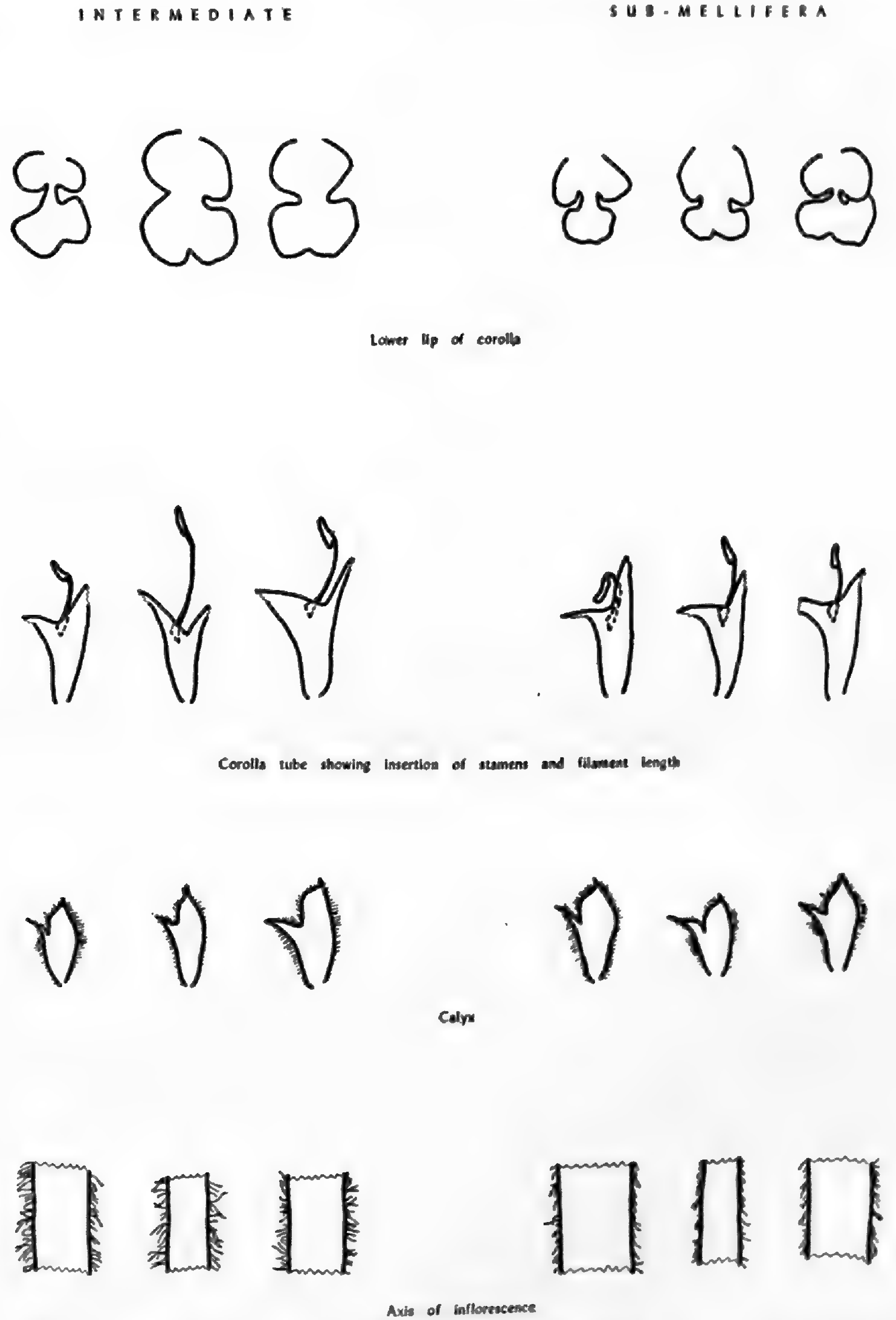


Fig. 2. Camera lucida drawings of three hybrids and three plants of probable hybrid ancestry from the "Olives" population; same scale and same portions of the flower as in fig. 1. Note the intermediacy of the plants at the left compared to those in fig. 1. The plants to the right, when compared with the examples of *S. mellifera*, are typical of the variation pattern produced by introgression. Note that though all three are similar to normal *S. mellifera*, they are more variable, and their slight departures from the average are mostly *in the direction of S. apiana*.

that species, from a second back-cross seven of whose ancestors came from it and one from S. *apiana*. Species (and subspecies) characteristically differ in many ways; a species difference seen as a whole is compounded of many things (Anderson, 1954). Differences in proportion are more common than differences in absolute size, while differences in change of proportion with size are even more characteristic. Pubescence *patterns* are as important as pubescence and color *patterns* are as important as differences in color. One needs to define in as exact terms as possible the totality of this difference so that it can be used with precision in population analysis. There are other Salvias in southern California besides S. *apiana* and S. *mellifera;* we need to understand the difference between S. *apiana* and S. *mellifera* so thoroughly that we can unhesitatingly distinguish between introgression of these two species and introgression of either of them with S. *clevelandii,* for instance. To do this job well requires repeated and exhaustive examination. The differences do not come with labels on them; as Linnaeus said long ago, "The characters are where you find them." A slipshod examination of the differences can produce nothing better than a slipshod interpretation of the population dynamics.

The characters eventually used (see fig. 1) were as follows:

(a) *The length of the lower lip of the corolla, measured to the nearest millimeter.*—This is precisely the character used by Epling.

(b) *Point of insertion of the stamens.*—In S. *mellifera* the stamens are inserted on the corolla well inside the tube; in S. *apiana* well outside. This character was scored in the following grades: well inside tube, barely in or barely out, well outside tube.

(c) *Pubescence of calyx.*—*Salvia mellifera* has coarse hairs on the calyx, particularly along the veins. The pubescence of S. *apiana* is so short and dense that it does not look like hairs at all, except under high magnification. The length of the longest hairs on the calyx was measured to the nearest millimeter.

(d) *Length of terminal spines on calyx.*—The calyx lobes of S. *mellifera* are tipped with long weak spines; in S. *apiana* the spines are so short as to be virtually invisible. This character was scored by measuring the spines at the tip of the upper lobes to the nearest millimeter.

(e) *Pubescence on the axis.*—Both S. *apiana* and S. *mellifera* have appressed pubescence on the axis of the inflorescence. In S. *mellifera* the hairs are pointed downwards; in S. *apiana* they point upwards. They were scored in the following grades: downward, outward, upward.

(f) *Length of filament,* measured to nearest millimeter.

FIELD STUDY

Hybridization between the two species was studied on the lower slopes of the San Gabriel Mountains above Arcadia, California. This site was originally chosen not for any special features but because (for the laboratory where the senior author was working) it was the closest spot at which the two Salvias could be found in profusion. They were studied mainly along a footpath which wound westwards (more or less on the contour) from the road up the Santa Anita Canyon. Less intensive field studies were carried on at several other locations. In this area the slope of the mountains is prevailingly toward the south. It is so steep as to approximate the pitch of a church roof, and the thin soil is stony with rock particles. As reported by Epling, though the two species frequently grow intermingled, *Salvia apiana* showed a preference for the drier sites. Along the steepest and jutting ridges, it grew in almost pure stands, while in shadier and moister spots along sections of the trail only *Salvia mellifera* was represented. The trail is one much used for recreational purposes and the vegetation along it has suffered repeated incursions from the public. Beer cans dot the landscape, particularly near the road. Half-formed side-trails are common, and the shrubs and larger perennials bear the scars of repeated vandalism. The site had been subject to disturbances for some decades, yet the flora as a whole was largely native. Out-and-out weeds were rare and the Salvias (at first glance) did not seem to have mongrelized at all. There were no apparent hybrids, and the casual impression was that for these two species one had nothing except typical specimens of *Salvia mellifera* and of *Salvia apiana.* The latter species, to be sure, is extremely variable, but the variations all tend in the direction of *Salvia apiana* var. *compacta* (see below) and seemingly have nothing to do with S. *mellifera.*

Closer plant-by-plant inspection did not quite bear out this conclusion. In one of the gullies, close to the point at which the path left the road, the vegetation bore the scars of intensive vandalism. Here there were a number of plants of S. *mellifera* which varied more from plant to plant than is typical for this species. Careful examination demonstrates (see below) that this variation (in so far as it is measurable) is all *in the direction of* S. *apiana* and presumably represents slight introgression from that species. A meticulous examination of every plant along the path indicated that introgression from S. *apiana,* so slight as scarcely to be apparent even to the experienced eye, had taken place at several points along the trail.

At one point, however, there had been much introgression, and this area was studied intensively. There were a few plants obviously intermediate between the two species, and others which were more or less like S. *apiana* or like S. *mellifera* but with color patterns, growth habits, corolla shapes, and inflorescences which were clearly atypical. It was not until the area had been repeatedly visited that it became evident that the hybrids and introgressants formed a compact population confined to a distinct area, only one corner of which abutted on the trail.

Even from the first examination it was evident that this area was at the point where the trail came down the farthest from the mountain side, to a spot once occupied by oaks. Gradually it was realized that the variants were confined to a space where some years ago the oaks had been cut and a small grove of olives had been planted. The olives had been abandoned but had continued to grow, and native vegetation had spread in around them. The upper corner of this area, which was crossed by the trail, had been used repeatedly for camping and some of the trees had been cut. It was in this doubly disturbed spot that most of the strangest-looking hybrids were found, but the entire area in among the abandoned olives, in so far as it had any Salvias, had nothing but atypical ones. Some of them were so grossly atypical as to be readily demonstrable as such in the pictorialized diagram (fig. 3) which takes account of only six measured characters. Some were so similar to *Salvia mellifera* that to demonstrate their introgressive origin would require careful scoring of such evanescent characters as flower color pattern and the angles at which the stamens are held.

ANALYSIS OF VARIATION

Collections were made from every plant abutting on the trail and from the area in among the olives. These were treated as two population samples, "path" and "olives." The data are presented as pictorialized scatter diagrams and as frequency distributions for a hybrid index based on these diagrams in figs. 3 and 4. Drawings to scale are shown in figs. 1 and 2 for a few representative plants. It will be seen that the population along the path is mostly composed of plants of the two species which show little or no indication of introgression but that a few of the S. *mellifera* showed slight introgression from S. *apiana,* about as much as we would expect in a second back-cross (i.e. in plants with seven ancestors from S. *mellifera* and one from S. *apiana*). The "Olives" population is clearly mongrel. Off-type plants are in the majority. Seen as a whole they represent the kind of criss-crossing recombinations of intermediate characters so typical of hybrid populations whether natural or artificial. In the area of the abandoned olive orchard such mongrels are clearly in the majority; had it been possible to score such characters as color pattern it would probably have been possible to demonstrate that they make up virtually the entire population.

Discussion

This example of introgression between S. *apiana* and S. *mellifera* is in some ways the most illuminating of the numerous examples of hybridization in natural populations which have been reported in recent years. Let us summarize the main points. Two species easily hybridized in the experimental plot do not ordinarily hybridize in the field, though they grow intermingled over wide areas. However, in a strange habitat (or collection of strange habitats) adjacent to their natural range, hybrids and their mongrel descendants press in to the virtual exclusion of the parental species. There are several important inferences which can be drawn from this example. The abundance of hybrids in the field, once a habitat is provided in which they are at an advantage, demonstrates that there is no barrier (as such) to hybridization between these species. Hybrids are virtually absent, not because they are not being produced but because when they do occur there is no place for them. The association of which these two Salvias are a part has been through the sieve of natural selection. All kinds of species in it have been continuously selected for getting on with each other; they form a multi-dimensional

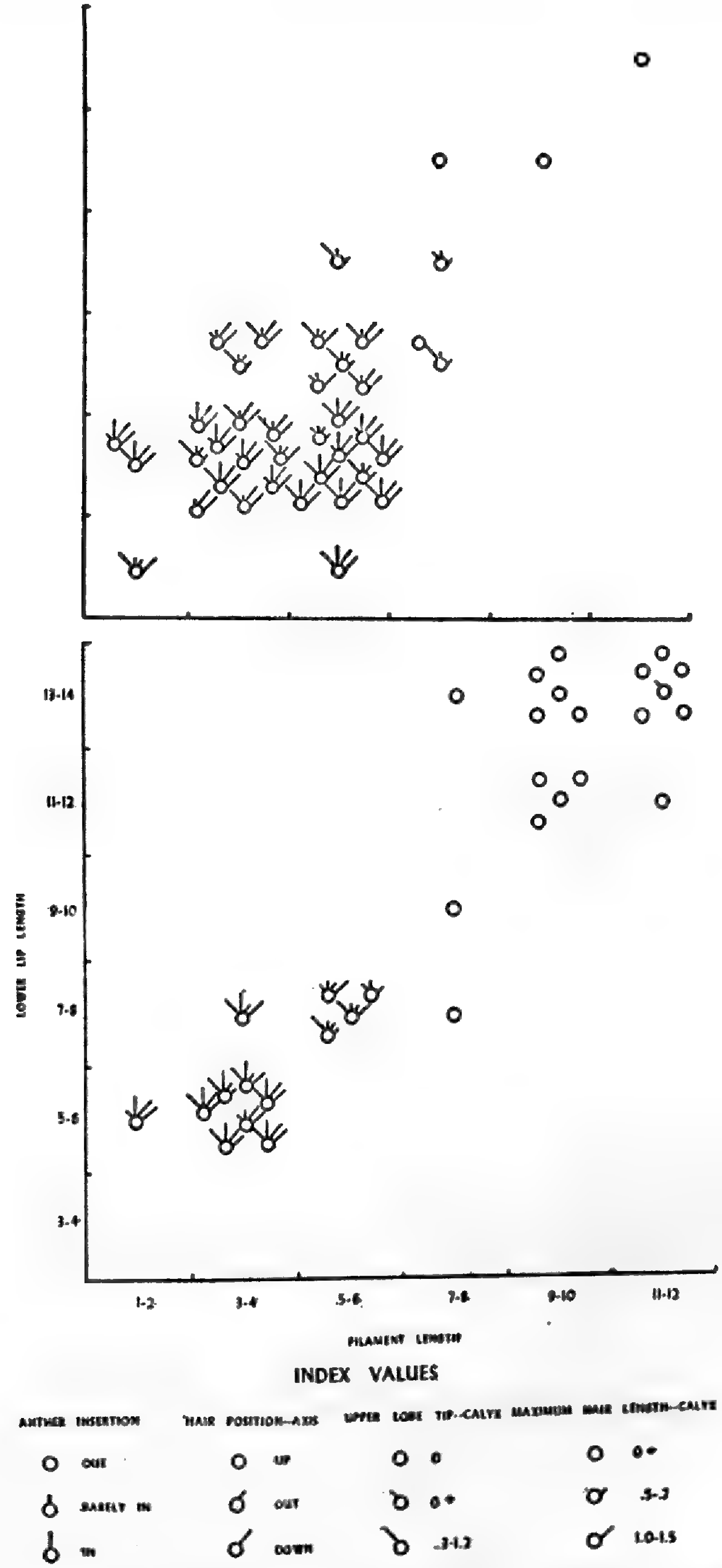


Fig. 3. Pictorialized scatter diagrams of two populations of *Salvia*; above "Olives" population, below "Path" population. Each circle illustrates a single plant. Lengths of filament and of corolla are measured and diagrammed the same in both populations, though indicated only in the lower example.

Fig. 4. The data of fig. 3, diagrammed as frequency distributions on a hybrid index which has values running from 0 for "good" *mellifera* to 12 for "good" *apiana*. Further explanation in the text.

jig-saw puzzle the pieces of which fit tightly together. There is no place in this closed association for an intermediate between any two species, or even for minor variants. It is not until a new ecological dominant, like man (Sauer, 1952), comes along and makes a set of radically new habitats that the hybrids can even demonstrate their presence readily. When this happens not only can they grow and persist but among their mongrel and variable descendants are various new recombinations, some of which are at a selective advantage in the relatively open associations produced by man.

By reference to only two of the most obvious physical variables, soil and sunshine, one can demonstrate what radically new habitats are presented by the olive orchard. Previously there had been dry sunny hillsides with pockets of soil, and shady oak woods with black woods soil. Cutting down the oaks and planting the olives produced pockets of sun, shade, and semi-shade on top of black woods soil. Planting out olives introduced an alien tree which, however, had been selected for such Mediterranean climates. On the other hand, the young trees were spaced out away from each other and from woody vegetation in a way quite unlike anything in the native woody flora. It was in these highly peculiar habitats that the variable progeny of the original hybrids had been at a selective advantage. Though we have no proof of the assumption, it seems likely that the hybrid progeny growing there are but a small and highly selected representation of the offspring originally seeded into the area.

It was Darlington (1939) who first pointed out clearly that the short-range and long-range effects of natural selection are almost diametrically opposed and that evolutionary systems which manage somehow to meet both these needs tend to be favored. The immediate need of the next generation is to conserve the adaptation already achieved. In a mature association this means producing offspring as much like the successful parent as possible. In such an association any surviving organism has fitted well into a particular niche; its offspring to succeed as well should have the same characteristics. The long-time need of the species, however, is for enough variability so that when changes arise in the physical and biological environment, the species is at length able to fit into a new niche, or even into new niches. Darlington pointed out how the side-by-side operation of apomictic and sexual reproductive systems in various plant genera allowed the successful individuals to produce, apomictically, offspring which were exact copies of the successful parent, though still retaining the capacity (by sexual reproduction) to produce variable descendants some few of which might be at a selective advantage in a changed or changing environment.

As more and more cases of introgressive hybridization have been analyzed, it has become increasingly clear that such genera as *Salvia* provide an almost ideal solution for this seemingly insoluble dilemma. It has been demonstrated repeatedly (and with increasing clarity) that hybrids and back-crosses are rare in natural populations not because of strong sexual barriers but because in mature associations of plants and animals which have evolved in each other's presence the whole association is closed. It is a complex interlocking system of mutually accommodating niches. Hybrids and back-crosses are absent not because they cannot arise but because when they do there is no place for them. Let man arrive and throw the whole association out of balance; let mammalian herbivores (as in New Zealand) be unleashed upon a vegetation with no previous experience of such beasts, and mongrel populations press into the new niches which have been created and themselves take part in building up a new interlocking system. Those genera, therefore, are at an over-all selective advantage which can build up complex barrier systems of exterior agents (in the wide sense) that protect the successful adaption from change so long as the association of which it is a part goes along its old ways, and yet can spawn hybrids and back-crosses in direct proportion to the breaking up of the old association. Genera with very strong internal barriers (such as complete hybrid sterility between well-differentiated taxa) would eventually perish under such changes and doubtless have.

Summary

1. Introgression between *Salvia apiana* and *Salvia mellifera* (previously studied in the field and in the breeding plot by Epling) was studied intensively in the San Gabriel Mountains.

2. As previously noted by Epling, the two species, though highly interfertile, intergrade only slightly or not at all, even when growing intermingled over very wide areas.

3. Extensive introgression was discovered in a small localized area. It proved to be an abortive olive orchard established some years ago among live oaks adjacent to the mountain side where the Salvias were native. Among these olive trees hybrids and back-crosses between these two species grew in abundance and even formed the bulk of the population.

4. The evolutionary significance of these facts is briefly discussed.

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INTROGRESSION IN ADENOSTOMA

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On any theory of evolution, differences between individuals are compounded somehow into specific and eventually into generic differences. An efficient analysis of plant-to-plant variation should give us critical data for determining the origin of the basic variability which is the raw material for evolution. If, as is currently generally believed, this basic variability results from gene mutation, then an efficient analysis of individual-to-individual differences should reveal the kind of local differentation pattern which might be explained on such an hypothesis.

For such studies *Adenostoma fasciculatum,* the common "chamise" of coastal California, is excellent material. Over a large part of its range, plant-to-plant variation is so conspicuous as to compel attention. In the hills behind Palo Alto or on the burned-over slopes of Mt. Diablo, virtually any three or four plants of *Adenostoma* chosen at random can be used to demonstrate the magnitude of this variation and its strongly germinal basis (figs. 1 and 2).

If we examine adjacent bushes of *Adenostoma* along a mountain pathway, it is easy to show that though they are growing so closely side by side that their branches interlock, we can readily distinguish the branches of any one bush by the general similarity of their inflorescences. Though parts of some bushes may be in the sun and parts in the shade, though some branches may be strong terminal leaders and others physiologically suppressed, all the branches on any bush have a "nucleus of common features," while the differences from one plant to another are always perceptible and are frequently conspicuous. If we choose a few good-sized bushes and remove the terminal inflorescences from each four to five well-developed branches from each and lay them in the pathway, an independent observer can easily determine from exactly which bush in the vicinity each set of branches was collected. By actual experiment it has been determined that under these conditions a class of students can match up a series of branches with a series of bushes without a single error. Any three such *Adenostoma* bushes are as different from each other as are three named varieties of lilacs in a collection in a botanical garden. Like the lilacs, they have a strong tendency for all the trusses of bloom on any one bush to be recognizably similar and yet for the trusses to vary perceptibly (and sometimes conspicuously) from one plant to another. Unlike the lilacs, however, the variation is largely confined to differences in the size and branching pattern of the inflorescence. Frequently this may be the only noticeable difference between adjacent bushes, though occasionally one may also find single plants which differ in height, in length of the leaves, in leaf shape, and (even more rarely) in the scurfiness or pubescence at the base of the calyx. Flower color, flower size, and flower shape are not noticeably different in any of the material.

Fig. 1

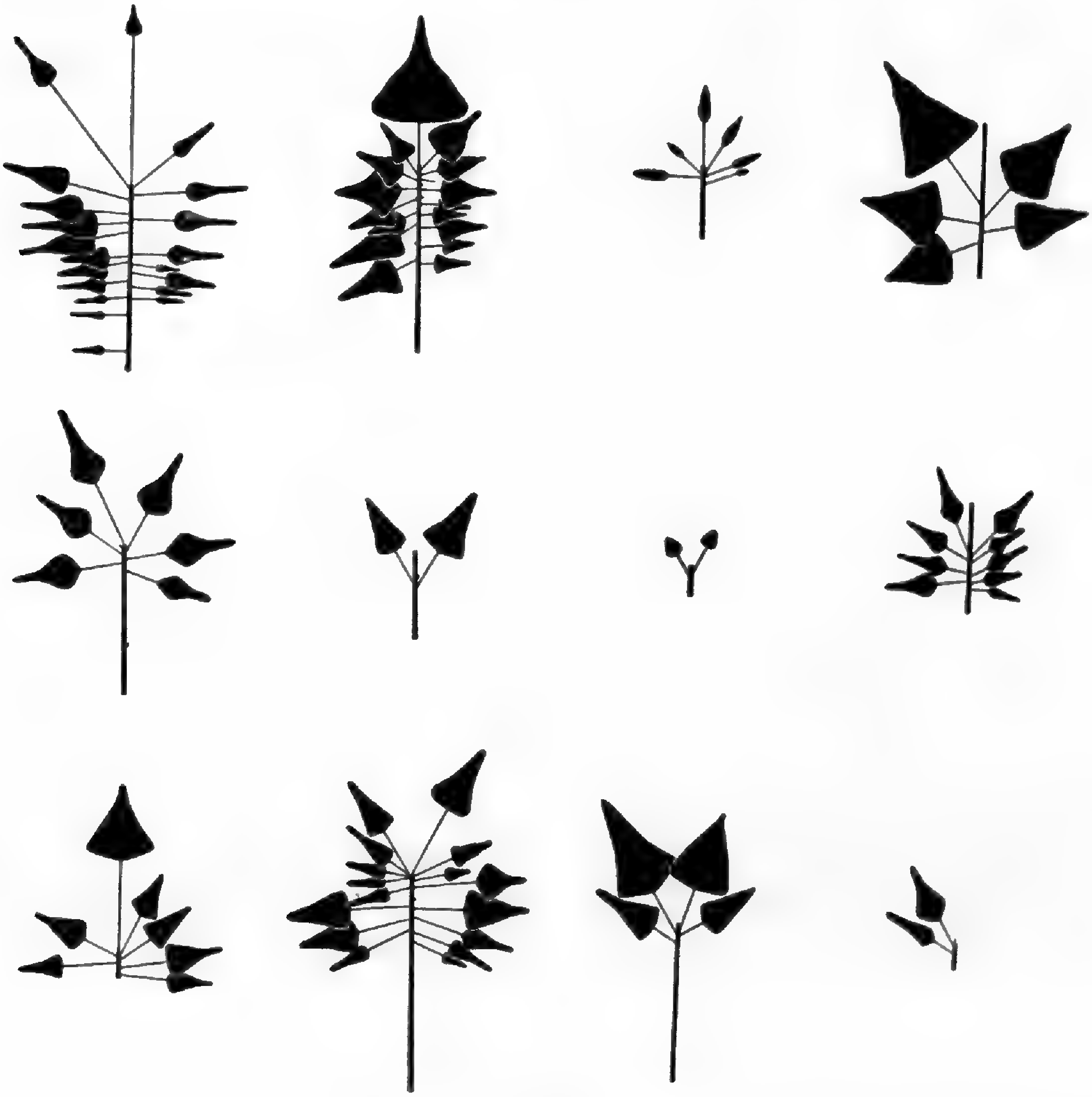

Fig. 2

Figs. 1 and 2. A comparison of inflorescence differences within plants and between plants in *Adenostoma*. Each drawing is a tracing of an actual specimen, and they are all printed to the same scale (× approximately .1). The heavy dark line in each separate figure represents the terminal portion of the previous year's growth (primary axis). The thinner lines departing from it are axes of the secondary inflorescences of this season's growth. The triangular to diamond-shaped masses are traces of the outline of ultimate inflorescences.

Fig. 1 (opposite page). Four branches per bush from five different and closely adjacent bushes (each horizontal row represents four different branches from the same bush).

Fig. 2 (above). One branch each from twelve different bushes of *Adenostoma*, printed to the same scale (× .1) and collected from the same general locality (west of Palo Alto golf course) as the branches illustrated in fig. 1. Note how much difference there is from bush to bush compared to the differences within each bush for such characters as: number of secondary inflorescences; length of peduncle; size and shape of ultimate inflorescences; extent to which terminal inflorescence is or is not differentiated from the other ultimate inflorescences.

A preliminary morphological examination demonstrated that the variability of the inflorescences can be broken down in terms of several quite different elementary variables. Taken all together, they produce at the one extreme a small inflorescence so highly condensed that the separate flowers are tightly packed together into one mass. At the other extreme, a large open panicle is made up of flowers well isolated from one another. The five elementary variables (see fig. 3) producing smaller, denser inflorescences are: (1) shorter internodes, (2) more secondary branches on the primary axis, (3) more flowers from a single node, (4) more telescoped nodes, (5) more branching of the fourth degree at the base of the tertiary branches. The larger, more open panicles, on the contrary, are produced by (1) longer internodes, (2) fewer secondary branches on the primary axis, (3) only one flower per node, (4) no telescoped nodes, (5) no evident branchlets at the base of the tertiary

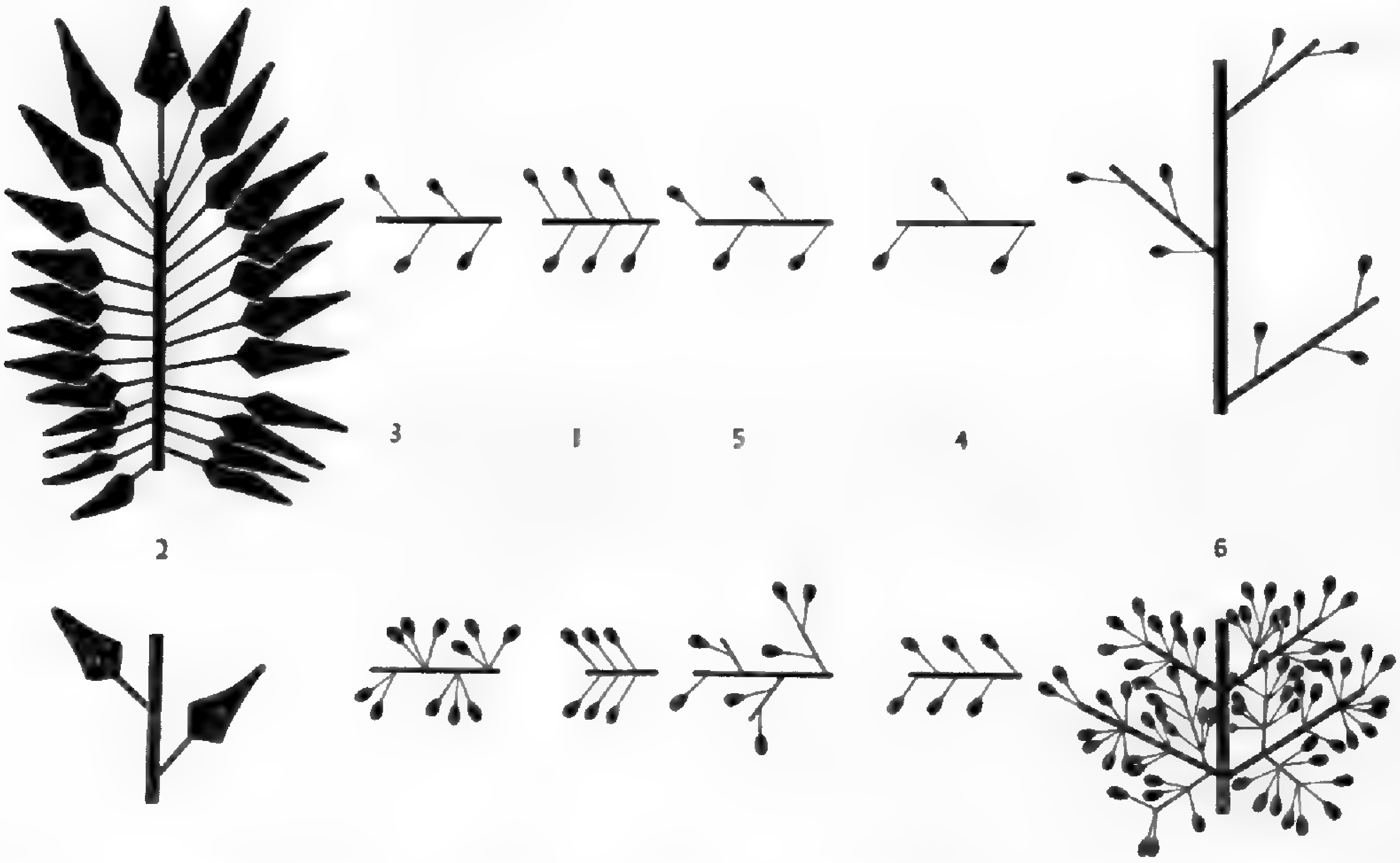

Fig. 3. Diagram showing the various components of inflorescence density in *Adenostoma*. These should be compared with fig. 4 which are tracings from actual inflorescences. The extremes ordinarily met with in the Palo Alto population are shown for each character, though the upper extreme for number of secondary inflorescences on the primary axis is too large for successful illustration and has been omitted. At the extreme left (No. 2) is illustrated the character of number of secondary inflorescences; below, two secondaries, above 25 secondaries. The four different components of density (Nos. 3, 1, 5, and 4) are illustrated from left to right; in each case the open extreme is shown above, the denser, below. No. 3, number of flowers per node; No. 1, number of telescoped internodes; No. 5, amount of branching of the fourth degree; No. 4, length of internode. At the right (No. 6) are shown comparable portions of two inflorescences combining all four factors for density of inflorescence. The diagram above the number *6* shows a small portion of an inflorescence which has simultaneously: only one flower per node; no telescoped nodes; no quaternary branching; long internodes. The one diagrammed below it shows simultaneously: several flowers per node; telescoped nodes; quaternary branching; and short internodes. In No. 6 the erect heavy line represents a portion of the secondary axis and the lines diverging from it are tertiary axes. As in Nos. 3, 1, 5, and 4, each small pear-shaped dot represents a single flower.

branches. These various elementary variables making for more or less density of the inflorescence are illustrated diagrammatically in figs. 3 and 4.

As is demonstrated in fig. 5, these five elementary variables, each in its own way making for a more or less open panicle, can recombine within wide limits. One may have many telescoped internodes with only a single flower at each internode, or one may have three or more flowers at each internode (incipient branching?) without any of the nodes being telescoped. Only when the total population sample is studied is it apparent that *on the average* the shorter internodes, the fewest secondary branches, the largest number of flowers per node, the telescoping of internodes, and the development of branches on the tertiaries all *tend* to occur together.

Fig. 4. Diagrams to scale (× .9) of flower number and arrangement in two actual inflorescences of *Adenostoma*. Though one is more open than the other, neither represents either the extreme of openness or of density realized in the Palo Alto population. The dense extreme, for instance, would look like a solid mass if diagrammed in this manner.

The more clearly one is able to apprehend the variation pattern of all these five variables, the more certain is it that their association is far from random. Let us, for example, consider precisely the chances of finding an individual plant which showed the extreme value for each of these five variables. If we merely consider the upper quarter of the population for any one character the chances of finding a plant which is as extreme as that is, of course, 1 in 4. For any two characters it is ¼ × ¼ or 1 in 16. The chances of finding a plant which is in the upper quartile for each of five characters is $(\frac{1}{4})^5$ or 1 in 1024. The chance of finding a single such plant in a collection made from 30 plants is 30/1024, about 1 in 34, if these characters *were not associated.* Actually three such plants were found in the very first collection, and such multiple extremes have been found in every population sample. When, as will be demonstrated below, the number of measured characters was increased to seven, extreme individuals which measured in the upper fourth of the distribution for each of these seven characters were still met with in every population though the chances of getting such an individual with random association of all seven characters is $(\frac{1}{4})^7$ or less than 1 in 16,000.

These variables were measured as follows:

Number of flowering secondary branches.—

The key to understanding variation in the inflorescences of *Adenostoma* turns on an extremely elementary point. We need to distinguish carefully between growth of the current season and of the previous one. The new growth has a more or less straw-colored surface; that of the previous season has darkened to gray. When attention is paid to this simple point one can readily distinguish comparable portions of the inflorescence. Until that is done he is apt to confuse a whole set of small inflorescences on a plant of the dense extreme with the widely separated branches of a single inflorescence in the opposite, open-flowered type (see fig. 2, for example). In the former there may be only one or two secondary inflorescences departing from the apical portion of any primary stem, while in the latter as many as 30 or 40 secondary branches will depart from the apical portion of each well-developed primary. In making the collections care was taken to choose a primary branch which was typical for the well-developed branches on that particular bush. Since there are ordinarily hundreds of such branches on any one bush, this can be done quickly and accurately. Preliminary trials were made to make sure that collections from the same set of bushes on different days produced essentially similar ratings.

Length of longest tertiary.—

From representative inflorescences, selected as described in the previous section, a representative secondary branch was selected as follows: On many plants all the secondary branches were closely similar; on some plants the terminal or the basal secondaries might be differentiated; on a very few plants there was a good deal of variation in the size and shape of the secondaries in any one inflorescence. A secondary branch was chosen from the mid-portion of the inflorescence for which

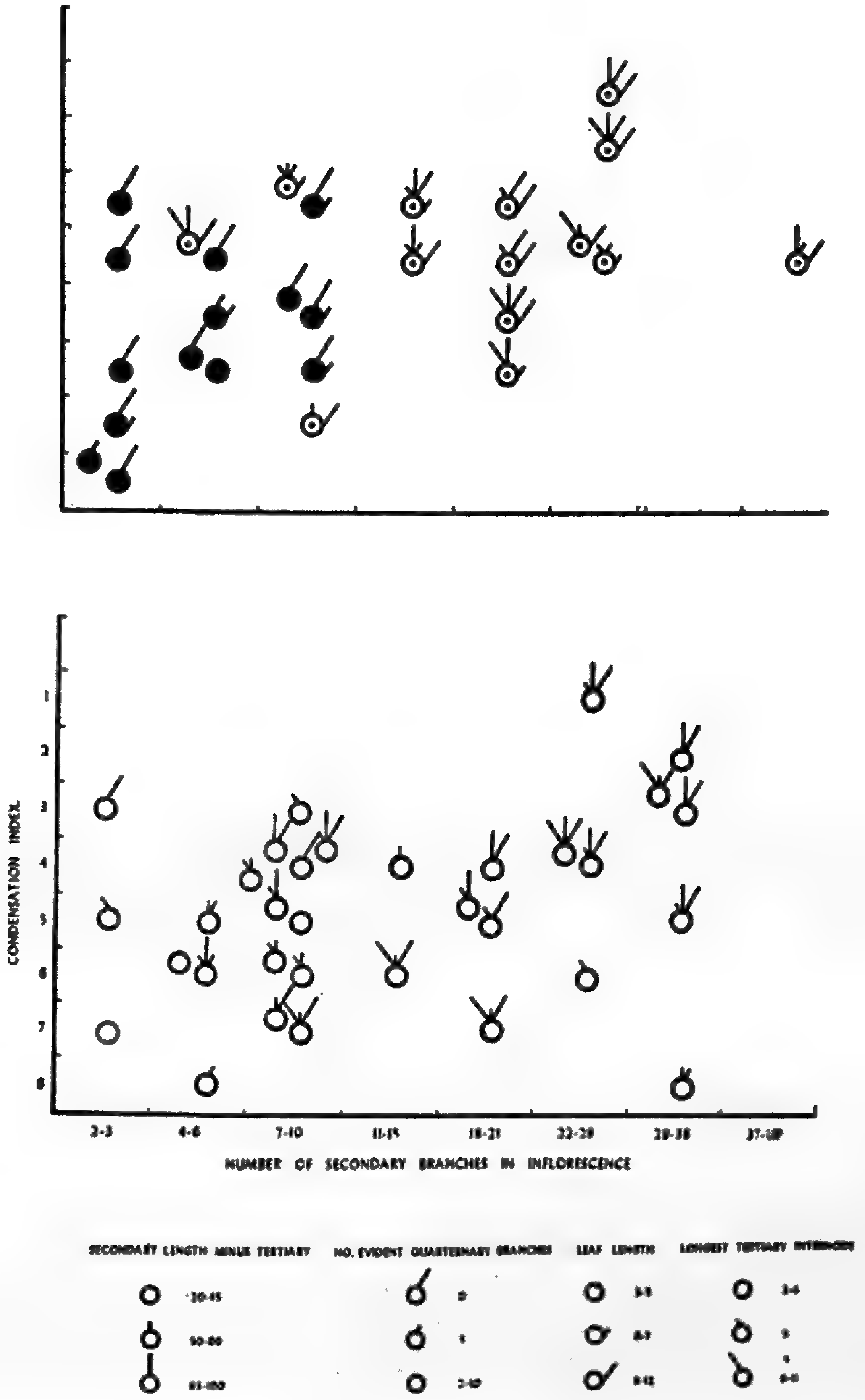

Fig. 5. Pictorialized scatter diagrams showing two collections of *Adenostoma* from Palo Alto. Below, random sample plus 1 or 2 selected extremes. Above, collection of every plant from a dry summit (solid black) and a collection of an equal number of plants from damper slopes among oak trees. In both diagrams the horizontal scale represents the number of secondary branches in the inflorescences. The vertical scale shows a condensation index from 1 (open) to 8 (very dense). This index combines two measures of density by adding the number of flowers per node to the number of condensed nodes out of five successive nodes.

there were several other secondaries matching it in size and shape (when, as in the dense extremes there were only one or two secondaries, then the least damaged one was chosen). The length of the longest tertiary on this selected secondary was measured with calipers and a steel ruler.

Length of the secondary inflorescence.—

A secondary inflorescence, chosen as previously described, was measured with calipers from its junction with the primary stem to its apex.

Longest tertiary internode.—

On the longest tertiary inflorescence previously chosen, the length of the longest internode was measured with calipers.

Number of flowers per node.—

The characteristic number of flowers at either side of each apparent node was recorded. Due to telescoping of successive nodes an apparent node might be two successive nodes, in which case there would be flowers on both sides of the stem. The number scored was that on one side. It varied from 1 to 3.

Number of condensed nodes.—

A tertiary branch chosen as described above was examined carefully at its base. Five successive apparent nodes were scored, and the number of these five nodes at which adjacent nodes had been telescoped was recorded. It varied from "0" in some plants (in which case there were no condensed internodes and the tertiary branch bore its flowers alternately) to "5" in which case condensation at each apparent node produced flowers borne oppositely at each node.

Number of evident quaternaries.—

Many of the selected tertiary branches bore no evident quaternary branches at the lowermost nodes. Among the dense extremes, however, quaternary branching was sometimes highly developed, and a few plants bore as many as 6 or 8 quaternary branchlets.

Leaf length.—

After the work was well advanced it was discovered that leaf length, though relatively uniform in some populations, varied widely and significantly throughout the species. It was accordingly measured with calipers by selecting typical leaves from each specimen.

Parenthetically, it may be worth noting that the chief variables in these inflorescences are surprisingly similar to some of those which differentiate the inflorescences of various races of maize. Condensation (the telescoping of successive nodes) was first described by me in *Zea Mays* (Anderson, 1944). I thought of it at the time as a phenomenon peculiar to cultivated cereals, a teratological abnormality which man had put to good use economically. Not till much later did I gradually come to realize that it is a widespread phenomenon among wild and cultivated species in various families of the flowering plants. I have detected it in *Dactylis*, *Cichorium*, and *Phlox*, in every instance as one of the results of hybridiza-

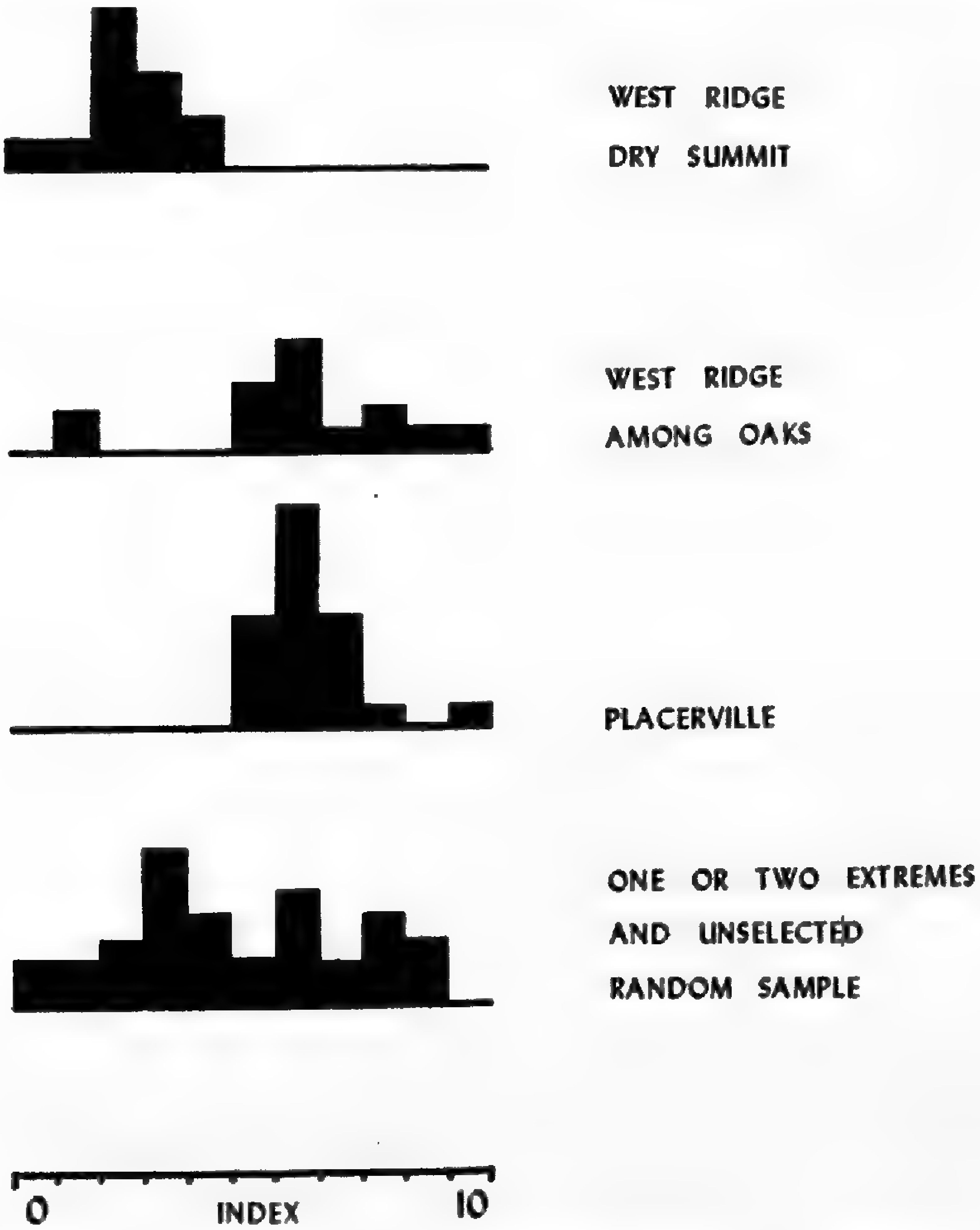

Fig. 6. The collections of fig. 5 plus an additional collection from Placerville ("mother lode"), diagrammed as frequencies on a hybrid index which runs from 0 for the low dense extreme to 10 for the tall open extreme. The index is formed by combining the five characters (the two characters used on the horizontal and vertical axes plus the three characters used on the rays), giving equal weight to each: lowest third, 0; middle third, 1; upper third, 2. A plant scored as 10, for instance, was in the upper third of the scale for each of the five characters.

tion between well-differentiated taxa. It is a phenomenon worthy of investigation by some one thoroughly conversant with the literature and concepts of plant morphology.

POPULATION STUDIES

As soon as the fundamental variables at the base of most of the variation in *Adenostoma* inflorescences had been apprehended, a large population was collected and analyzed. This was selected slightly west of Stanford University, at one of the localities where W. S. Cooper made his classical studies of the chaparral over thirty years earlier. Here the chaparral clothes many acres of rolling upland, the general appearance being surprisingly close to that of a British moorland. *Adenostoma fasciculatum* was the commonest species in this association and in some areas composed virtually all the shrubby vegetation.

An attempt was made to make as random a selection as possible. Surveyor's lines had been cut through the chaparral. These were followed on foot, and inflorescences, one to a plant, were selected roughly every ten or fifteen feet. Care was taken to select an inflorescence from a vigorous branch and one that was representative of the plant from which it was taken. The results are presented as a pictorialized scatter diagram in fig. 5. Those desiring an elementary exposition of this graphical device will find one in Anderson, 1952, with a minimum of technical phraseology. A technical discussion of the basic philosophy underlying the technique has recently been published (Anderson, 1954).

From fig. 5 it is clear that all the measurable plant-to-plant variation in this population sample is in two closely knit complexes with various intermediates and recombinations. At the one extreme is a small dense inflorescence, the individual flowers so closely set together as to be indistinguishable without careful examination. The inflorescences are tiny but may be scattered in large numbers over the surface of the bush. At the other extreme are big plumy inflorescences something like open panicles of lilacs. They are held high above the bushes on wand-like branches and are so open that the individual flowers are clearly recognizable as such at first glance.

By the method of extrapolated correlates (Anderson, 1949) it is possible to draw up precise technical descriptions of the taxa responsible for such introgressive complexes as this one in *Adenostoma.* Without further information one would have no means of knowing whether he was looking for a taxon more extreme than the "large open", or one more extreme than the "small dense", or perhaps for both. At just this point in the investigation Dr. G. Ledyard Stebbins (who had been following the investigation with much interest) brought me a population sample from the "mother lode" country at the base of the mountains on the *east* side of the great central valley of California. This proved to be made up exclusively of the large open-panicled extremes, the general average of the entire collection made by Stebbins, being about equal to the most extreme plants in the random collection from Palo Alto. The simplest hypothesis (since this taxon was apparently in existence in another part of California) was that the *Adenostoma* of the coastal chaparral, the *Adenostoma* we had been studying, represented extensive introgression of the same open-panicled sort by a low dense kind even more extreme than the lowest and densest which had turned up in the random sample. I then drew up a description of this hypothetical extreme, character by character, adding a few more characters from the examination of the lowest-densest extremes from the random collection. Theoretically, we should hope to find a low bush *Adenostoma,* with short leaves, with expanded blades, not so needle-like as those we had been studying. It should have extremely dense inflorescences, borne as single panicles of the current season's growth, the entire inflorescence no larger than the end of a man's thumb. The hypanthium (the lower surface of the bloom) should be pubescent. This description was then run down in Jepson's *Flora,* just as though we had the specimen at hand. It led to *Adenostoma fasciculatum* var. *obtusifolium.* Jepson's description answered our extrapolation in all respects except that it made no mention of pubescence. Examination of typical specimens of var. *obtusifolium* in the Dudley Herbarium at Stanford University showed that just such a pubescence was indeed found in this variety.

Adenostoma fasciculatum var. *obtusifolium* is a characteristic plant of the Channel Islands and a few rocky headlands along the southern coast of California. According to our interpretation, the highly variable Adenostomas of the coastal chaparral resulted from extensive introgression of a tall plumy *Adenostoma,* similar to those now growing in the oak savannahs of the "mother lode" country, with this low shrub from foggy headlands along the coast. Each of these had its own contribution to make to life in coastal California. The latter was accustomed to growing in shallow, rocky soil, under intense radiation, with virtually no shade, but with abundant rain and frequent fog and drizzle. The former was accustomed to deep soil and partial shade, but it was bred to dry air, extensive seasons of extreme drought, and to baking heat.

With this new understanding I returned to the locality in which the original collection had been made. The basic ecology of the site almost fell into place at once, when interpreted in the light of this analysis of variation in *Adenostoma.* The low extremes were growing on rocky, thin-soil summits or on little ridges. The big plumy ones were on north slopes, particularly in those spots where there was water seepage in the early spring. The strangest of the bizarre recombinations were to be found in the semi-abandoned corral back of an old ranch, where man and his animals had made strange new ecological niches in the edge of the chaparral. Two collections were made from two extreme habitats and are shown in figs. 5 and 6. For the first collection every plant was sampled on a rocky little ridge; the second was made from moist spots in the shade of oaks at the northern edge of the chaparral, both sites being within the area where the original random collection was made. It will be seen that the populations of these two extreme habitats are outside the range of variation of each other and that the tall plumy extremes are fairly equivalent, on the whole, to Dr. Stebbins' collection from the "mother lode" country, at Placerville.

By the time these collections were analyzed, my term as a Visiting Stanford Professor had come to a close, and it was not possible to make further field studies of these plants. There remains to point out the bearing of this technical analysis on the general problem of the chaparral and its origin.

It is known from paleontological evidence that habitats similar to the oak savannah of the "mother lode" country and the coastal headlands of southern California had a history going back at least into the Tertiary. Chaparral vegetation is relatively new. There are those, like Carl Sauer, who view it as largely post-human; an ecological artifact brought about by large scale burning. There are others who admit that it has been strongly influenced by man but believe the chaparral, though relatively recent, to be definitely pre-human. The studies reported above do not settle this argument but they do present a new set of techniques by which significant data can be gathered for solving such problems.

As my field studies of *Adenostoma* drew to a close, I came to realize that the chaparral, as a whole, is made up not only of introgressive complexes of *Adenostoma* but of other genera as well. Of all the samples of the world's vegetations with which I have had personal experience it is, as a whole, the most wildly variable collection of intergrading complexes. It is variable, plastic, and at the present moment is vigorously differentiating into new types and sub-types under the impact of man, "an ecological dominant" (Sauer, 1952). To the student of evolution it presents an enormous outdoors experimental plot in which one can study not only the catalyzing effect of man upon the chaparral; it is a laboratory in which can be investigated the special problems of *all* such floras thrown into flux, of rapid evolutionary change as the result not merely of man but of any ecological dominant. The evolutionary problems of the California chaparral are essentially similar to those of the first land plants, to the evolution of floras under the impact of the first great herbivores, to the special problems of any of those times of rapid catastrophic impingment of one set of organisms upon another (Anderson and Stebbins, 1954).

The studies reported here were carried out in May and June of 1952 when I was Visiting Professor of Biology at Stanford University. I am greatly indebted to Dr. Twitty and various members of the departments for many courtesies and to Dr. Richard Holm and the staff of the Dudley Herbarium for technical help, tactful forebearance, and stimulating companionship.

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SOME AMERICAN ARBORESCENT LYCOPOD FRUCTIFICATIONS[1]

CHARLES J. FELIX[2]

INTRODUCTION

Among the more abundant elements of Carboniferous fossil floras are the fructifications of the arborescent lycopods. Although usually detached, specimens in organic connection with vegetative stems have been found, and there is considerable information available for the various organ genera to which they have been assigned. The strobili present a varied assemblage consisting of bisporangiate specimens and unisporangiate ones containing either microspores or megaspores.

A problem confronting the worker is the identification of microsporangiate fructifications. The megasporangiate ones do not pose a comparable problem, for diagnostic generic characters are usually well-defined, and recent spore studies have contributed materially to a better comprehension of generic boundaries.

Lepidostrobus, Lepidocarpon, Mazocarpon, and *Sigillariostrobus* have generally been accepted as being well defined, with the first three well represented in North American petrifactions, but it is probable that many microsporangiate representatives of these now bear erroneous names. Inasmuch as the fructifications are seldom found attached to vegetative correlatives, identification depends upon characters of the cones. For example, there is evidence that all cones of *Lepidostrobus* may be bisexual, but a number of microsporangiate strobili have been assigned to the genus. Thus, the worker must distinguish these from microsporangiate cones which are definitely known to represent the other three genera listed above. This has proven, in a number of instances, to be rather difficult, and generic limits are not as strongly defined as previously considered. Structurally, these four genera are rather similar in consisting of a central axis bearing whorled or spirally arranged sporophylls, each with a single sporangium on the upper surface. The size range is variable and not a reliable criterion for identification.

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[1] An investigation carried out in the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] United States Geological Survey, Coal Geology Laboratory, Ohio State University, Columbus, Ohio.

The present study is undertaken with the object of clarifying generic limits of American representatives and of presenting new material which will increase our knowledge of the various cone genera.

The genus *Lepidostrobus*, a uniform one in most respects, is the most abundant American lycopod strobilus. Several species found in the petrified state both in Europe and North America are fairly well known, but in North America the majority of specimens reported have been preserved as impressions and compressions, only a small number of petrifactions having been described. The fragmentary and poorly preserved condition of the specimens has rendered it difficult to define specific limits with the clarity desired. *Lepidostrobus* has become a rather general repository for cones believed to have been borne on *Lepidodendron*. It is a heterogeneous assemblage in which specific limitations are difficult to determine and in all probability may include more than one genus. Consequently, the student of the lepidostrobi is confronted by Williamson's ('93) statement: "I have for many years endeavoured to discover some specific character by which different Lepidostrobi could be distinguished and identified, but thus far my efforts have been unsuccessful."

This study of American lepidostrobi is not intended to be monographic in scope. Rather it represents an analysis of several American fossils whose mode of preservation has revealed anatomical and spore characteristics of possible value in defining generic limits. The number of American species preserved as petrifactions and casts is small in comparison to the number known from Europe, yet the American group includes a varied and distinct assemblage.

Lepidostrobus is an elliptical or cylindrical cone varying from less than 1 cm. to more than 7 cm. in diameter, and from 3 cm. to possibly 50 cm. in length. Structurally, it consists of a central axis with sporophylls arranged spirally or whorled. The stele may or may not be medullated and has a typically lepidodendroid xylem cylinder. Each sporophyll bears a single sac-like sporangium attached its full length to the upper surface by a narrow base. The microsporangia are borne on the upper sporophylls and megasporangia on the lower.

A sizeable collection of cone material has been accumulated in this laboratory in recent years. Specimens of *Lepidostrobus* constituting a new species occurred in great abundance and were in such excellent preservation as to afford valuable information on spore and other anatomical features of the genus. Several specimens are closely comparable to *Lepidocarpon* microsporangiate cones and add to our limited knowledge of these fructifications. In addition various data on other American strobili are compiled.

The specimens came from Mineral, Kansas, and New Delta and Nashville, Illinois, but the most prolific source was the Petersburg V coal north of Booneville, Indiana.

Lepidostrobus has received extensive treatment. Early descriptions were given by Hooker (1848) and by Binney (1871). Notable anatomical studies were made by Maslen ('99) and A. Arber ('14), while the upper Carboniferous British impression species were reclassified by E. A. N. Arber ('22), who used the shape of the sporophyll as a specific unit of classification.

Lepidostrobus Brownii (Unger) Schpr. is one of the most studied members of the genus. Bower ('93) made a detailed study of the axis, while Zeiller ('09, '14) contributed noteworthy anatomical studies of the species. In North America several species based on compression and impression materials have been described, but only in recent years has attention been turned to lepidostrobi preserved by other means. *Lepidostrobus coulteri* Coulter & Land is regarded as the first petrified example (Tilton, '12). Several other species, including two new ones presented in this paper, have since been described and have contributed materially to our knowledge of the genus.

Description of New Species

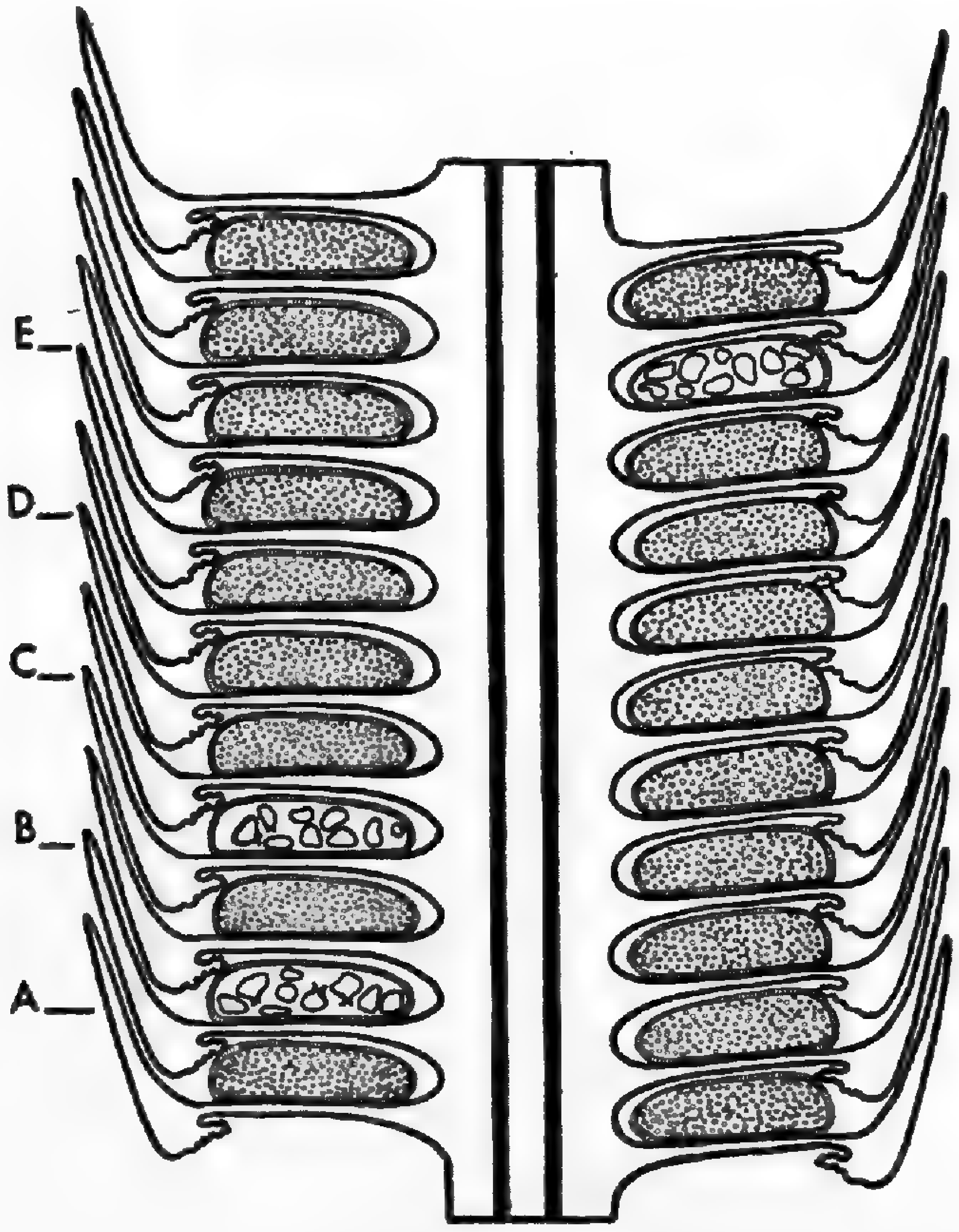
Lepidostrobus **diversus** Felix, sp. nov.

This species is based on several specimens in coal balls from the Petersburg V coal near Booneville, Indiana. Numerous strobili, or fragments of them, were found in several coal balls, one yielding several scores of cone axes.

Three specimens are cited as the type and are supplemented by information obtained from eleven others. They were mostly incomplete, but several basal and apical portions were available, and one cone (pl. 14, fig. 7) probably represented an entire strobilus. Five specimens contained megaspores only, four were bisexual, and the remainder contained only microspores. Over a score of fragmented and sporeless specimens furnished data on axial and sporophyll anatomy. None of the specimens were found attached to vegetative shoots, but the longest cone measured 11.2 cm. in length. The maximum diameter never exceeded 1 cm., indicating a long, slender cone. In more complete cones tapering did not start until approximately 6 mm. from the apex, and then it was abrupt to an acuminate tip covered by the laminae.

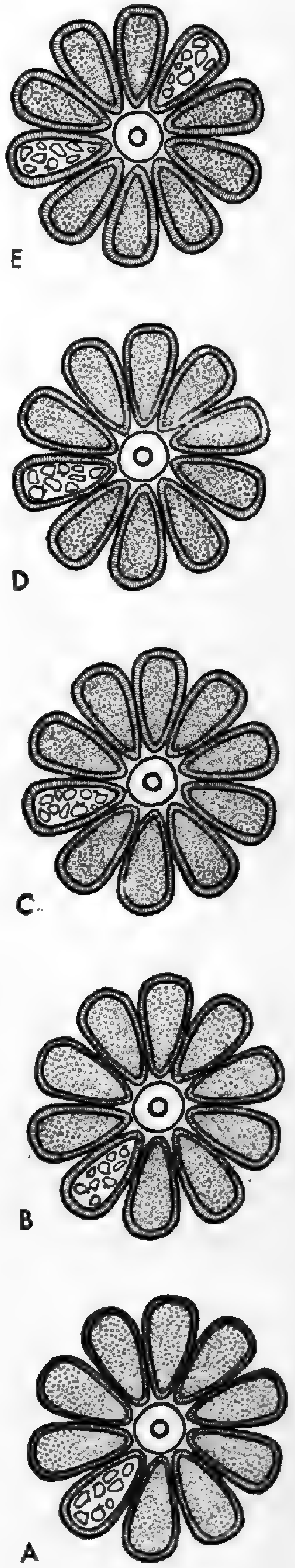
The cones of this species are bisexual with the usual arrangement of megasporangia on the lower sporophylls and microsporangia on the upper ones. An interesting feature is the occurrence of a transition zone, containing both mega- and microsporangia, between the basal megaspore (fig. 12) and apical microspore regions.

The Transition Zone.—A feature somewhat similar to the transition zone has been reported in *Lepidostrobus russelianus* Binney (Chaloner, '53b), and it probably occurs in other lepidostrobi, poor preservation usually limiting observation. *L. diversus* differs from *L. russelianus* in having a zone of intermixed sporangia, best shown in specimens 825 and 857. In the latter clearly delimited alternating zones of megaspores and microspores occurred between the lower megaspore and upper microspore zones. The full length of the zone was not definitely determined due to the fragmentary nature of material, and in more intact specimens the basal sporangia had dehisced.



Text-fig. 1

Text-fig. 1. Diagrammatic drawing of longisection from transition zone of *Lepidostrobus diversus.* WCB 857. A–E indicates sections where megasporangia occurred.



Text-fig. 2

Text-fig. 2. Transverse sections from transition zone of *L. diversus.* WCB 857. A–E relate to comparable sections in text-fig. 1.

In specimen 857 six megasporangia were encountered in a space of nine spirals. The megasporangia did not appear in any regular sequence other than occurring in alternate spirals. Only one megasporangium was present in each, with the exception of the sixth which contained two (pl. 13, fig. 5; text-fig. 2E).

The first megasporangium is shown in fig. 1 (pl. 13) and represents section A in text-figs. 1 and 2. Portions of eleven megaspores are visible in the next highest megasporangium in fig. 2, which corresponds to section B of text-figs. 1 and 2. A third sporangium is revealed by section C, and three megasporangia become visible in longi-section (fig. 3), with the basalmost one being the single one shown in fig. 2 and text-fig. 2B. A fourth megasporangium of the spirals is produced by section D and is the uppermost one in pl. 13, figs. 3 and 4; the basal sporangium of figs. 2 and 3 has passed out of the plane of section, and the megasporangia figured in fig. 4 are the two upper ones of fig. 3; and, although in alternate spirals, the obliqueness of the section tends to make them appear to be in adjacent ones. The only spiral of the transition zone containing two megasporangia is the sixth one shown by section E of text-fig. 2 and in fig. 5 of pl. 13; the fifth megasporangium is the uppermost on the left side of the axis, the sixth appearing on the right side of the axis (fig. 5); the lowermost megasporangium of fig. 5 is the upper one shown in fig. 4.

The Axis.—Most of the cone axes measured about 2 mm. in diameter, and possessed a stele composed of primary wood and a small pith. Cortical tissue was seldom preserved. The more complete specimens showed variation in axis diameters from 1.2 × 1.5 mm. to 1.8 × 2.9 mm. The stele itself varies from a protostele of 250 μ in diameter to a siphonostele of as much as 500 μ, the latter containing a pith 60 to 200 μ in diameter.

TABLE I

MEASUREMENTS OF VARIOUS ANATOMICAL COMPONENTS OF SEVERAL SPECIMENS

Specimen	Spores in transverse section	Axis diameters (mm.)	Xylem diameters (μ)	Pith diameters (μ)	Xylem width (μ)	Cone diameters (mm.)
810 B/T3	Microspores	1.9 x 2.5	283 x 336	110 x 114	88	4 x 9
811 A/T2	Microspores	2.1 x 2.6	336 x 356	116 x 132	110	6 x 9
816 AA/T1	Microspores	1.8 x 1.9	367 x 375	66 x 101	107	6 x 11
816 AA/B1	Microspores	1.9 x 2.2	367 x 448	None	—	4 x 9
857 B-4	Mega- and microspores	1.3 x 1.8	331 x 362	178 x 224	110	6.9
806 B/T4	Microspores	1.8 x 1.2	240	63	84	5 x 7
846-1	Megaspores	1.2 x 2.4	398 x 510	219 x 275	127	5.5 x 12

The basal regions of the cones contained no pith, and it appears that medullation did not occur until almost half the length of the axis. The pith cavity gradually increased in size, reaching its maximum diameter near the apex. Table I shows the wide variation with regard to size and anatomy of the axes.

In medullated steles the xylem was ringed by a row of exarch protoxylem elements 6–18 μ in diameter. Within these there are usually four rows of metaxylem cells 22–45 μ in diameter, with the largest cells restricted to the two innermost rows.

It has been pointed out frequently that size and stelar anatomy are features of the lycopods which must be treated with caution (Arnold, '40; Felix, '52). Several species of *Lepidodendron* and *Lepidostrobus* have been described in which the feature of a protostele or siphonostele has been considered as diagnostic (Hirmer, '27; Mathews, '40). However, it is becoming more apparent, as our knowledge of this group increases, that the xylem-pith relationship is often determined by ontogeny.

Specimen 816 (pl. 14, fig. 7), the most complete encountered, gave some explanation for variations observed (Table II). Here there was some increase in stele diameter from the base to the apex, and most of the cone was protostelic, developing a pith only in the upper microsporangiate region. Campos ('25) found a similar situation in *Lepidostrobus Masleni* in which the axis diameter decreased from base to apex, while the pith diameter increased. The entire cone was medullated, but the possibility that its basalmost portion was missing would account for the failure of a transition to a protostele.

TABLE II

ANATOMICAL MEASUREMENTS OF A SPECIMEN AT DIFFERENT LEVELS

	816 A1 73 mm. from apex	816 A3 46 mm. from apex	816 A4 6 mm. from apex
Axis diameters (mm.)	1.8 x 2.9	1.7 x 2.5	1.8 x 2.1
Xylem diameters (μ)	357 x 428.4	311 x 357	331.5 x 357
Pith diameters (μ)	None	None	76.5 x 112.2

The Sporangia.—The sporangia show no significant departure from that characteristic of *Lepidostrobus*. They are radially elongate and attached adaxially on the narrow pedicel. In tangential sections they are bag-shaped, broader than the pedicel, and overlapping it. They are 3–3.5 mm. long, 0.7–0.9 mm. high, and 2–2.5 mm. wide when mature. Near the cone's apex they decrease progressively, and sporangia 0.5 × 2.0 mm. contain spores in tetrads. The palisade wall cells of micro- and megasporangia appear identical, varying from 45 μ in the upper side to 65 μ near the pedicel.

A small plate of sterile tissue occurs in mature sporangia (fig. 10). Arising from the base of the sporangium, it is attached radially along the pedicel and frequently presents a T-shaped process. Such a sterile plate is of common occurrence in lycopod cones.

The Sporophylls.—These are attached to the axis in close spirals, usually 10 sporophylls in each. Specimen 816 had 49 spiral revolutions in 83 mm. of cone exposed in sectioning. The adaxial angle of the sporophylls to the axis is about 90°. It was noted that different angles of attachment were found on the same axis, some pedicels being borne at right angles and some pedicels and sporangia arched. This arching has been interpreted as a specific character (Hirmer, '27, p. 191; Hoskins and Cross, '40, p. 424), but here it is evidently caused by varying degrees of distortion. Different angles of sporophyll inclination have been observed in other species, and it was probably a character of the living plant in some instances and not a result of compression. *Lepidostrobus noei* shows such a condition, and Mathews ('40) considered the normal inclination to be near 90°, but in the lower portion of the cone it was 70° and in the upper part 80°.

The length of pedicel from its point of attachment to the axis to the point where it turns upward as a lamina, is about 3.5 mm. Near the apex, pedicels as short as 2 mm. often bear sporangia with mature microspores, and basal ones may attain a length of 4 mm. The pedicel is triangular in cross-section at its point of departure from the axis (fig. 8), being approximately 530 μ in width, 460μ in height, and without an elongated dorsal keel, and as it continues its distal course it becomes flattened laterally. At a distance of about 1.5 mm. from the axis the average width is approximately 900 μ and the height 350 μ, and the entire pedicel is bordered by dark, thick-walled cells. Here the vascular trace is surrounded by a sheath 200 μ in diameter, composed of thin-walled undifferentiated cells. These have a tendency to break down, leaving a round cavity. Often a large gap forms beneath the vascular bundle as a result of the disintegration of these cells. There is no evidence of phloem.

The pedicel wings begin to take form midway between axis and lamina, and the width and height both increase (fig. 9). At 3 mm. from the axis the width is about 2.2 mm. and height 0.57 mm., with 0.30 mm. of the height composed of a rounded heel about 0.24 mm. wide at its widest point. At the distal end of the pedicel, near its juncture with the lamina, a maximum width of 4.8 mm. and a height of 0.52 mm. is reached, 0.44 mm. being the length of the heel. Thus the pedicel is broadly flared out at its distal end (fig. 10), and here the dark, thick-walled cells are restricted to the pedicel wings. At this point the pedicel continues upward as a lamina (fig. 6). The lamina is considerably thickened (0.43 mm.) at its juncture with the pedicel and tapers to an acuminate tip. The maximum length is about 6 mm., but near the apex of the cone it may be 2–3.5 mm. long.

At the junction of the lamina and pedicel is a downward projection of the sporophyll, commonly called the "heel". This structure is usually present in *Lepidostrobus* but is absent in the two well-known American species *L. imbricatus* and *L. noei.* The heel in *L. diversus* has an appearance quite different from that of species previously described. It ranges from 300 to 500 μ in length, is variously lobed, and as many as three or four additional and shorter projections often extend downward from the pedicel behind the principal distal portion (fig. 6).

The course of the sporophyll trace is unusual enough to warrant attention. In the majority of lycopod cones the traces originate from the stele at an acute angle and maintain this path into the sporophyll. An exception is *L. Binneyanus* reported by Arber ('14), where the sporophyll traces follow an obliquely downward direction in the distal portion of their course from stele to sporophyll pedicel. In *L. diversus* the trace makes the usual departure from the stele at an acute angle. This course is maintained upward through the inner cortex for about 600 μ; a downward bend of about 70 μ occurs before it resumes its upward course through the outer cortex (fig. 11). The trace appears to enter the second spiral above its point of origin, and it always enters the outer cortex at a point opposite the sporophyll below the one which it ultimately enters.

The trace maintains a horizontal course through the pedicel near the adaxial side. It is composed of a mesarch bundle of about 15 scalariform elements and measures 25–35 μ in diameter. At no point during its horizontal course through the pedicel are transfusion cells associated with the vascular trace or seen to run into the sterile plates of tissue of the sporangia. Distal to the sporangial attachment and in the region of the lobed heel, the trace curves downward and then turns up into the lamina. This downward curve is the "dorsal loop", a feature observed in several lycopod fructifications. The tracheids of the trace are scalariform, and in the dorsal loop and the upturned lamina they are accompanied by several scalariform transfusion tracheids.

Despite excellent preservation in several specimens, there was no evidence of a ligule or ligular pit on the sporophyll.

The Megaspores.—Megaspores of *L. diversus* were abundant, several scores of megasporangia being available for study. The spore count of 16 in each sporangium was confirmed by serial peels and by maceration; by maceration technique spores were loosened from the matrix with dilute hydrochloric acid and removed individually from the sporangium with a 00 artist's brush.

The spores are referable to the Lagenicula section of *Triletes* and conform most closely to *Triletes rugosus* (Loose) Schopf. The separation of *T. rugosus* from *T. translucens* is not too well defined. Schopf ('38b) assigned spores to *T. rugosus* on the basis of a slightly smaller size, thicker spore coat, and coarse surface texture. Dijkstra ('46) assigned them both to *T. rugosus.*

The spores of *L. diversus* are longest in the axial dimension, and prominent apical flaps and arcuate ridges are present (figs. 17–19). The spore surface is rugose. However, in reflected light it appears coarser than it actually is (fig. 19) due to differences in lights and shadows encountered in photographing; also the adherence of some dirt particles render it difficult to distinguish essential features. The walls averaged about 10 μ in thickness, ranging from 8.5 to 15 μ. The diameter in the axial dimension was 645–795 μ in macerated material. In measurements made from peels the diameters were 400–800 μ.

There has been some confusion in the nomenclature of the apical segments of megaspores of the Lagenicula section. Schopf ('38b) defined as vestibule: "the structure thus formed consisting of the elongated and upraised apical portions of the three pyramic segments." In *Triletes rugosus* he stated that no vestibule could be detected. Arnold ('50) and Chaloner ('53b) have chosen to use the term "apical prominence" to describe the neck-like projection characterizing the Lagenicula section. The elongate spores of *L. diversus* have such an apical prominence formed by expansions of the contact faces (figs. 18, 19); it ranges from 315 to 380 μ high from the apex to the well-developed arcuate ridges. The suture lines are 240–300 μ long and are delimited distally by arcuate ridges.

Aggregates of tiny globules are frequently found adhering to the megaspore wall (fig. 13). Chaloner ('53b) reported similar aggregates of cuticular material on spores of *T. rugosus* from *Lepidostrobus olryi* and *L. russelianus* and on *Triletes horridus* from *Lepidostrobus dubius.* Arnold ('50) described scattered, minute papillae on *Lagenicula rugosa* (*Triletes rugosus* of Dijkstra); their occurrence was so sporadic that he did not consider it a sufficient basis for specific separation. The appendages on spores of *L. diversus* also occur sporadically, being absent on some spores and occurring irregularly in others. They range up to 10 μ in diameter. These were probably more abundant than the number attached to the spores would indicate. Numerous round globular bodies varying in diameter from 2 to 10 μ occur in all the megasporangia. Resembling fungal spores, they number hundreds in some sporangia and appear identical to the globules attached to the spore walls.

An examination of several specimens suggests that the aggregates of globules may serve as an aid in determining heterospory. Specimen 816 is 112 mm. long, 83 mm. of which was exposed in a radial cut (fig. 7); the remaining 29 mm. was not visible due to its oblique direction in the rock matrix. The upper 26 mm. of the cone is composed of microsporangia while numerous microspores are visible in most of the remaining dehisced sporangia, and to all appearances the cone is microsporangiate. None of these sporangia contained the cuticular globules. At 44 mm. from the cone's apex in about the 35th spiral, empty sporangia first appear containing large numbers of the globular bodies which were associated with megaspores in other cones. They continue to appear at irregular intervals, indicating a transition zone as in specimen 857 (figs. 1–5). At 73 mm. from the apex, sectioning of the cone revealed a sporangium containing megaspores.

Specimen 898 was an incomplete cone section 29 mm. in length with apical and basal regions missing. It was cut in a near-radial plane, and preliminary examination indicated it to be microsporangiate and composed of 22 spirals; the sporangia of the topmost three spirals are filled with microspores. Although dehisced, the next ten spirals of sporangia contained enough microspores to indicate their microsporangiate nature. None of these contained the globular bodies. The remaining sporangia were empty, and the cone presented the same microsporous appearance as did the basal portion of specimen 816. However, in the twentieth spiral serial peels revealed a sporangium containing megaspores referable to *Triletes rugosus* and hundreds of the globular bodies as well as about a score of microspores. Some of the spores were still in tetrads probably having filtered in from other sporangia. A microsporangium in the same spiral was almost filled with microspores but there was not a single example of the globular bodies.

In specimens 825 and 857 all megasporangia were found to contain large numbers of the globules in the transition zones but there were none in the microsporangia. Over 100 megasporangia were examined and found to contain the bodies. Of the hundreds of microsporangia examined, very rarely would a scattering of the globules be found in a dehisced sporangium containing a few microspores. When preservation apparently took place before dehiscence, the bodies were never present within microsporangia.

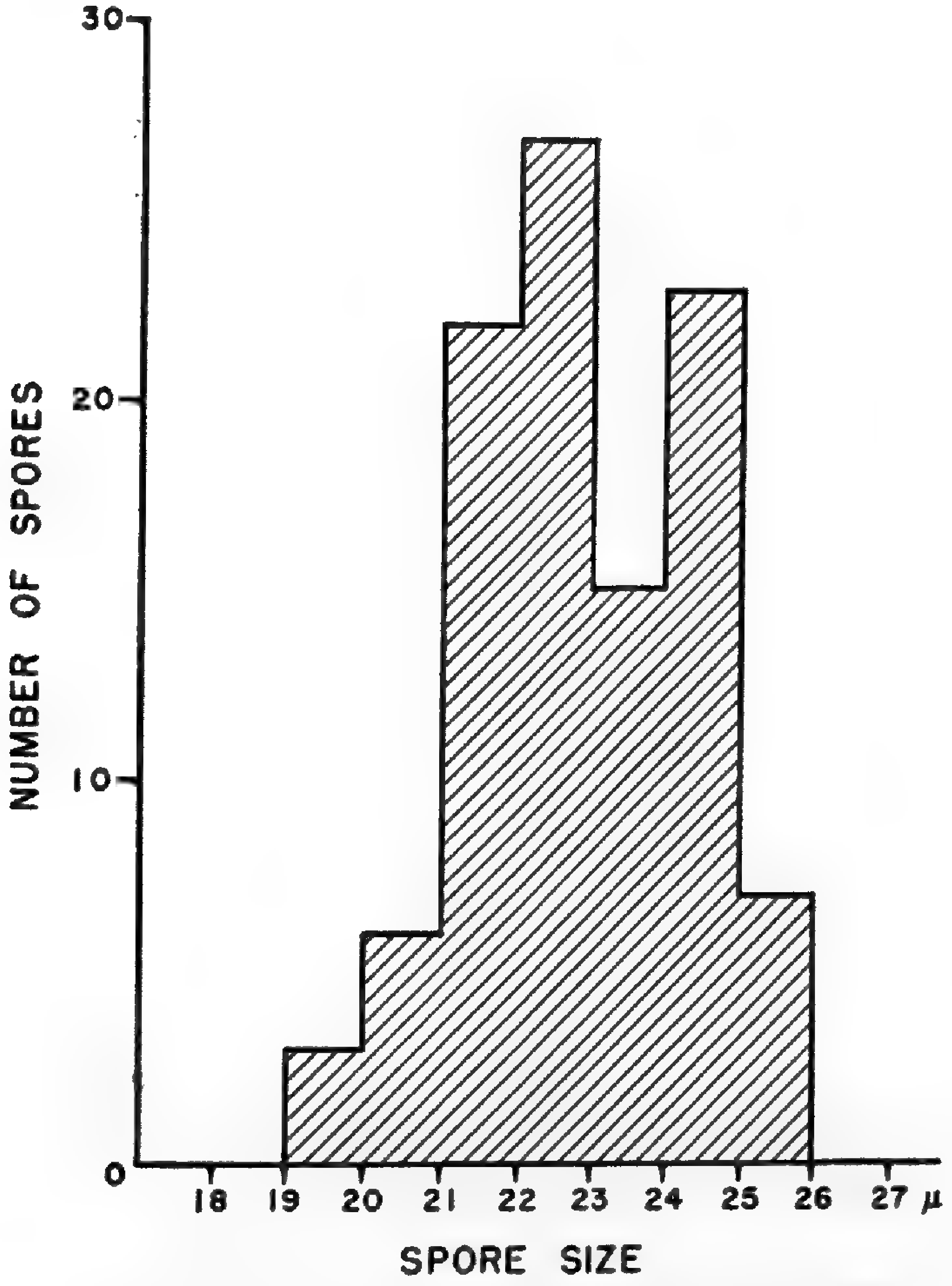
Lepidostrobus noei, an American species in which heterospory has been confirmed, was examined. The megaspores were densely coated with tiny globules 6–10 μ in diameter (fig. 23). The megasporangia contained numerous loose, globular yellow bodies identical to those on the spore wall and similar to those found in megasporangia of *L. diversus*. The microsporangia of *L. noei* did not contain these bodies.

Zeiller ('14) observed minute bodies 3–5 μ in diameter in sporangia of *Lepidostrobus Brownii*. He considered them to be fungal spores but was unable to find any evidence of mycelia. Zeiller reported them as occurring in both megasporangia and microsporangia (p. 40), but his figs. 10 and 20, pl. XI, which show large numbers of them, are of megasporangia.

It is not to be inferred that these cuticular globules can serve as indicators of bisexuality in all cones, but they appear to be reliable where mature mega- and microsporangia are available in the same cone. Their use is limited in that microsporangia occasionally do contain them. They could possibly be tapetal in origin. The immature microsporangia at the cone tip are composed almost entirely of a large subarchesporial pad and contain many large yellow, segmented globular bodies 5–20 μ in diameter; no microspores are present. In successively lower sporangia these segmented bodies break up into small yellow ones similar to the cuticular globules of the megasporangia; simultaneously tetrads of microspores begin to appear. In each successive spiral there is an acropetalous decrease in the yellow globules and a corresponding increase in the number of mature microspores. At the fifth or sixth spiral from the apex the bodies are no longer present and the microsporangia contain only mature microspores.

Bocheński ('39) found similar small granular bodies associated with the microspores in several *Sigillaria* microsporangiate cones. The fact that the spores were in tetrads suggests that the granules might have a tapetal origin.

The Microspores.—The spores, which are referable to *Lycospora,* occurred frequently in tetrads and many microspores are apparently immature. Those described were assumed to be mature, and uniform populations occurred in several specimens (text-figs. 3, 4).

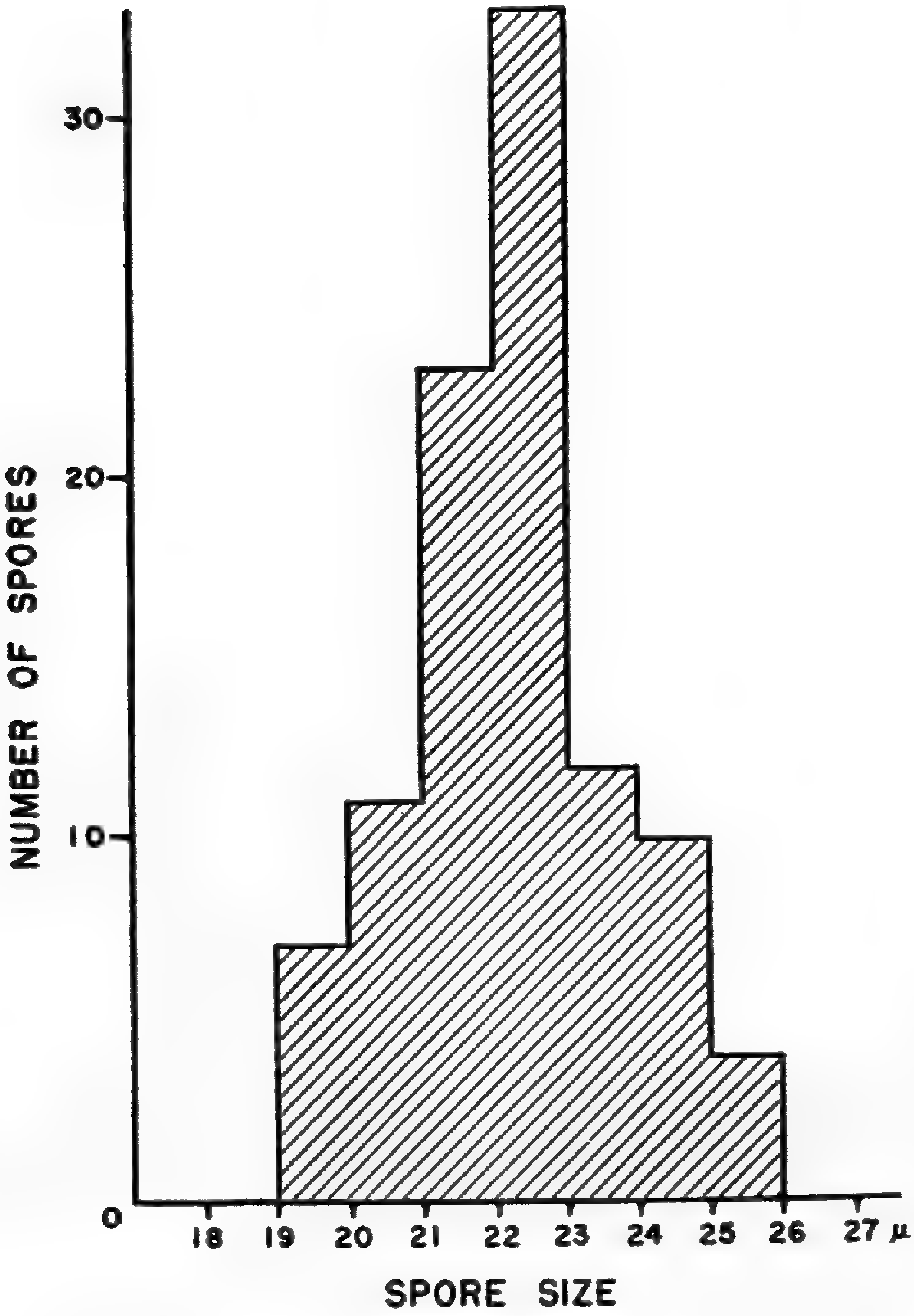


Text-fig. 3. Histogram of microspore size in *Lepidostrobus diversus* from a population of 100 mature spores. WCB 857.

The spores are radial, trilete, and roundly triangular in the transverse plane (figs. 14–16); the holotype measured 22.8 μ in diameter although other spores range from 19.2 to 25.8 μ. A narrow but distinct equatorial ridge was present, generally 1.2 μ in width, deviating to 1.5 μ in only a few instances. The rays are 8–11.5 μ long, and most of them appear to extend to the equatorial ridge. The lips are slightly elevated and about 1 μ wide with a thin but distinct commissure visible. The spore coat is slightly punctuate on proximal and distal surfaces and 1 μ thick. No previously isolated spores of *Lycospora* appear to be conspecific with those of *L. diversus*, although *Lycospora rugosa* (Schemel, '51), which occurs in the Des Moines series, has a similar size range but a slightly wider ridge and a granulose to rugose ornamentation.

Associations.—Associated lycopod stem remains were scarce. Five specimens of *Lepidodendron scleroticum* Pannell were found, several specimens of *L. serratum* Felix, and some small (5 mm. diameter) unidentified *Lepidodendron* stems. There is no evidence to indicate that any of these bore the *L. diversus* cones.

Diagnosis.—Cone slender, less than 1 cm. in diameter, approximately 12 cm. long; axis about 2 mm. in diameter, medullated apically but often protostelic



Text-fig. 4. Histogram of microspore size in *Lepidostrobus diversus* from a population of 100 mature spores. WCB 816 A4.

basally; sporophylls arranged spirally, usually 10 per revolution; sporophyll trace bending downward when entering outer cortex, a departure from normal steep upward course; bisexual with microsporangia at apex and megasporangia at base, a transition zone of intermixed mega- and microsporangia between two zones; megaspores 16 to sporangium, 645–795 μ in diameter, assignable to *Triletes rugosus;* microspores numerous, small, 19–26 μ in diameter, mildly punctate with equatorial ridge 1.2 μ wide, assignable to *Lycospora;* ligule not observed.

Locality and Horizon.—Strip mine near Booneville, Indiana; Petersburg V coal, Des Moines series, middle Pennsylvanian.

Type specimens.—WCB 816, WCB 818, and WCB 857, Washington University, St. Louis, Missouri.

LEPIDOSTROBUS **pulvinatus** Felix, sp. nov.

This description is based upon a single specimen in a coal ball from Mineral, Kansas. It was in excellent state of preservation and only slightly altered by compression (fig. 24). It measured 2 × 3.7 cm. in diameter and 5 cm. in length. This represents only a portion of a large lycopod fructification.

The sporangia, all containing microspores, possess a massive parenchymatous tissue developed to a greater degree than has been observed in any lycopod strobilus other than the megasporangiate one of *Mazocarpon*. The specimen represents the most significant lycopod fructification found in Mineral coal balls. The paucity of such cones has been made more apparent by the fact that the arborescent lycopods were one of the most abundant elements (Andrews, '51; Felix, '52), and probably no American coal ball deposit has produced larger quantities of *Lepidodendron.*

Stelar Characters.—The central vascular cylinder is enclosed by the tissue of the axis, little cortical tissue being preserved. The stele measures 1.3 × 2.2 mm. in diameter, the pith being 0.46 × 1.4 mm. in diameter. There is no evidence of tracheidal cells in the pith.

The xylem width is about 380 μ. The metaxylem is five rows in width with the larger cells 65–85 μ in diameter and the protoxylem elements 11–15 μ. The large xylem elements possess wall thickenings which depart slightly from a strict scalariform arrangement. The bars are 3.5–4.2 μ thick and branch quite regularly to present a somewhat reticulate appearance such as is often found in lycopods but only to a limited degree. *L. pulvinatus* differs in that most metaxylem elements show this feature. "Williamson's striations" are present in all xylem elements.

The Sporophylls.—The sporophylls form a close spiral about the axis, and the angle of attachment is about 90°. The pedicel is about 16 mm. long from axis to lamina. It increases laterally from about 1.2 mm. near the axis to a maximum width of some 3.5 mm. at a point 2 mm. from the distal end. The upturned lamina measures over 17 mm.

The trace originates from the stele at an acute angle, maintaining this course to the sporophyll. In its course through the pedicel it is mesarch and composed of 20–25 xylem elements which average 60–85 μ in diameter. It is accompanied by numerous transfusion cells, and all trace elements are surrounded by a sheath 45–75 μ wide composed of thin-walled cells. The protoxylem cells are 6–7 μ in diameter; those of the metaxylem 13–20 μ.

Parichnos strands run the length of the pedicel, one on either side of the trace. They are formed at the proximal end of the pedicel by a bifurcation of parenchymatous tissue accompanying the trace. The strands are 160–205 μ in diameter, each composed of 10–12 large thin-walled cells 35 × 45 μ to 44 × 66 μ in diameter. The parichnos is adjacent to the parenchymatous tissue of the sporangium and often difficult to distinguish due to similarity of their tissues.

Although a ligular pit appeared to be present on some sporophylls, no definite ligulate structure was observed.

The Sporangia.—The sporangia have the radially elongated, narrow attachment to the pedicel characteristic of the lycopods. They are about 14 mm. long and 3.5–4 mm. high. They taper from 1.2 mm. wide adjacent to the axis to 5 mm. near the distal end, and are somewhat wedge-shaped when viewed transversely (fig. 28). Each sporangium is attached to the pedicel by a narrow neck of tissue about 65 μ in height and 175 μ in width. The sporangia are covered with the palisade layer of cells characteristic of *Lepidostrobus.* The prismatic cell layer varies in thickness; it is thicker at the base (75–90 μ), but near the top the sporangium wall is noticeably thinner (30–35 μ).

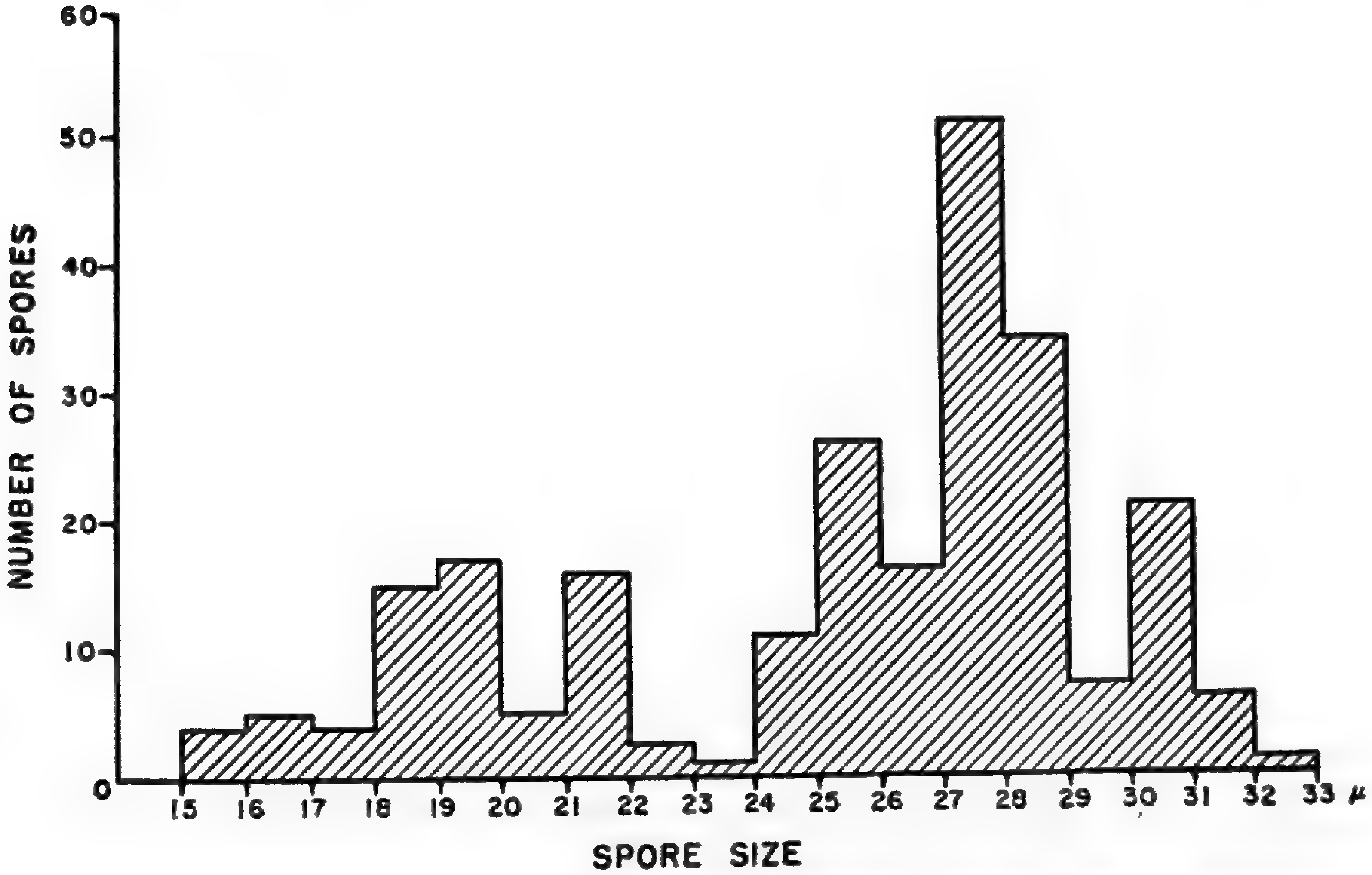
The amount of parenchymatous tissue in the sporangia is a prominent feature; it may appear as a T-shaped plate or swollen pad nearly filling the sporangium (figs. 25–28), or it may be entirely absent. It is not as regular a feature as in the megasporangiate *Mazocarpon* but nevertheless of frequent occurrence in apparently mature sporangia. In those sporangia showing considerable amounts of tissue the pad often extends 3.7 mm. into the sporangium and nearly fills it laterally. The basal cells of the pad are loosely arranged, irregular in shape (fig. 29), and measure 40 × 217–102 × 170 μ. Cells in the upper part of the pad are smaller, more compactly arranged, and more nearly isodiametric (fig. 30), being 54.5 × 68–80 × 85 μ in diameters. Many lateral plate-like branches occur, and large groups of spores are often almost completely embedded in the central bulk (figs. 25, 26). Several layers of elongate thin-walled cells are preserved internal to the columnar cells of the sporangial wall. These layers apparently line the entire sporangium wall and are 75–90 μ wide in various sporangia.

Several of the sporangia show a development of the central plates of tissue which extend across them in a manner similar to the trabeculae of *Isoetes* (figs. 27, 28). In *Isoetes* these are a result of sterile cells which form in the sporogenous tissue. Here the irregular development of lateral plates appears to be due to a breakdown of the parenchymatous tissue. No spores or abortive material are ever present in the cavities.

Bower ('03, p. 197) has pointed out the various conditions in which sporangeous tissue occurs in living spore producers. In many plants disorganization of a portion of the tissue occurs without becoming fertile (forming tetrads) and the subsequent absorption of the cells by the developing spores. Too, the sterile cells often persist as permanent tissue, sometimes forming partial or even complete septa.

There have been numerous arguments, based upon comparisons of habit, leaves, stem, and underground organs, in favor of the derivation of *Isoetes* from the Lepidodendraceae. Bower favored the derivation of *Isoetes* from the Lepidodendraceae due to the resemblance between the trabeculae of *Isoetes* and the sterile plates of tissue of lepidostrobi sporangia. The sterile plates of lepidostrobi originate from the subarchesporial pad as outgrowths and show no connection with the upper sporangial wall, as do the trabeculae of *Isoetes* which result from sterilization of potentially sporogenous tissue.

The Spores.—All of the sporangia contained microspores which were assignable to *Lycospora,* and spores from a single sporangium showed considerable variation (pl. 17, figs. 32–45). Spores in the upper part of a sporangium above the central pad were abortive in appearance. Usually withered, they were mixed with large numbers of globular, resin-like bodies. A considerable number from this region



Text-fig. 5. Histogram of microspore size in *Lepidostrobus pulvinatus* from a population of 250 spores obtained from a single sporangium. WCB 917.

were among the smallest isolated but showed distinct, and presumably mature, ornamentation features, ridges, and sutures (figs. 39–41).

The spore size varied widely (text-fig. 5). The largest spores occurred at the base in the sporangium (figs. 31, 34); their preservation was poorest, and they were compacted into dense masses often nearly completely enveloped by lateral projections of the central tissue. A large population consisted of probably mature spores whose diameter ranged from 25 to 31 μ (figs. 32, 35, 45). About 60 per cent of the spores were in this group. The spore coat was 1.2 μ thick, and the equatorial ridge 3.6–4 μ wide. The spores were coarsely punctate proximally and distally. In many instances a slight translucence was visible along the outer border of the ridge. Sutures were 9–12 μ long, 1.2 μ wide, with narrow commissures and slightly elevated lips.

Approximately 10 per cent of the spores had a size range of from 15 to 19 μ in diameter (figs. 40–42). The larger spores described above are evidently the normal mature form; however, if found isolated, this smaller group would probably be considered mature inasmuch as the spores are not withered or shriveled as they would be if abortive. Ornamentation is distinct, and well-developed equatorial ridges and rays are present. The ornamentation is coarsely punctate proximally and distally as on the largest spores. The equatorial ridge is often lacking on these smaller forms (fig. 42), but when present it is 1.2–1.5 μ wide, occasionally 2 μ, and slightly translucent on the outer margin. The cell wall is about 1 μ thick. The rays are 6.0–7.2 μ long and 1.2 μ wide, with narrow commissures and slightly raised lips. A considerable number of spores in a range of 25–29 μ had no visible ridge (fig. 33). However, they usually had a withered or shriveled appearance as if atrophied, perhaps accounting for the absence of an equatorial appendage.

Probably 15 to 20 per cent of the sporangial contents are clearly aborted spores and brown globular bodies similar to those seen in immature sporangia of *L. diversus*. Several tetrads occurred in the upper part of the sporangia. These often appeared to be large spores (fig. 43) until seen breaking up (fig. 44).

If found isolated, it is probable that the microspores of *L. pulvinatus* might be assigned to more than one species of *Lycospora*. Among the species diagnosed, the size range of *Lycospora parva* Kosanke (25.1–32.5 μ) is nearest that of the larger population of *Lepidostrobus pulvinatus*. However, their ornamentation and ridge features differ greatly, and there is little likelihood that they are conspecific.

The smaller population of *L. pulvinatus* most closely resembles *Lycospora micropapillatus* (Wilson & Coe) S. W. & B. (15–16 μ) in size and also in many emphytic features. Since most diagnosed species of *Lycospora* and those isolated from known cone species are far larger than *L. micropapillatus*, it is possible that the latter represents immature or aborted specimens such as occur in *L. pulvinatus*.

Discussion.—The assignment of this specimen to *Lepidostrobus* is admittedly questionable, but the great abundance of material from the type locality may eventually afford more tangible evidence of its true affinities. The *Lycospora* type spores are probably not restricted to *Lepidostrobus* alone, yet the unusual sporangia of *L. pulvinatus* offer no close comparison with microsporangiate cones of other lycopod genera. There is also the distinct possibility that the basal megasporangiate region is missing; thus tentatively *Lepidostrobus* appears to be the only genus acceptable.

Diagnosis.—Cone large, incomplete, 2 × 3.7 cm. in diameter; stele 1.3 × 2.2 mm. in diameter, pith 0.46 × 1.4 mm. in diameter and composed of thin-walled cells; sporophylls spirally arranged, prominent parichnos strands running the length of the pedicel; sporangia usually nearly filled with a massive parenchymatous pad which often breaks down to form trabeculae; only microspores present, assignable to *Lycospora* and ranging from 15–33 μ in diameter; no ligule observed.

Locality and Horizon.—Strip mine of the Pittsburg and Midway Coal Company, Cherokee County, Kansas; Fleming coal, Cherokee group, Des Moines series, middle Pennsylvanian.

Type Specimen.—WCB 917, Washington University, St. Louis, Missouri.

RESUMÉ OF PREVIOUSLY DESCRIBED AMERICAN SPECIES

LEPIDOSTROBUS ARRECTUS Hoskins & Cross, in Amer. Midl. Nat. 29:542. 1943.

Lepidostrobus aristatus Hoskins & Cross, in Amer. Midl. Nat. 24:421–436, *figs. 3–4, 12, 16.* 1940.

Cone.—Medium-sized, 11.5 × 2.7 cm. Incomplete, both ends missing. Preserved as cast in fine sandstone.

Axis.—Five mm. in diameter throughout known length. Eleven sporophyll bases on axis when viewed in cross-section. Cellular detail not preserved.

Sporophylls.—Arranged spirally, about 11 per revolution and 43 revolutions observed. Adaxial angle of pedicel to axis slightly greater than right angle. Pedicel 1.1 cm. long. Prominent stalk-like sporophyll bases about 1 mm. long on axis. Laminae very wide at base (3–4 mm.), 30–40 mm. long, a portion subtended prominently below the horizontal plane of the pedicel and slightly thickened, tapering rather gradually from wide base to an attenuated tip, closely appressed for the lower half but slightly divergent above, aristate in appearance.

Ligule.—Presence questionable. Indefinite structure arises from distal end of pedicel.

Sporangia.—Borne adaxially on sporophylls, closely crowded, 1 cm. long, wedge-shaped in top view, narrow, but not triangular in cross-section next to axis, broader and somewhat rectangular-ovate at distal end. Narrower pedicel broadly overlapped by sporangia. Apparently attached to sporophyll throughout length by narrow band of tissue.

Spores.—Two sizes found by macerating sporangia: 27 μ and 160–190 μ. Hoskins and Cross compared the megaspores with those of *Lepidostrobus Gallowayi* (Arnold, '33), but the only similarity was in size. A re-examination of megaspores of *L. Gallowayi* has shown that in Arnold's original diagnosis they were probably too small. The spores of *L. arrectus* were not examined in the course of this study, the type slides no longer being extant.

Locality and Horizon.—Pocahontas sandstone, lower Pottsville series, Pennsylvanian system. Six miles northwest of Orleans, Orange County, Indiana; Whetstone quarry.

Material.—One specimen, exposed by splitting sandstone block. Holotype, B-624-section 1 of holotype; B-625-section 2 of holotype. Paleobotanical Museum, Botany Department, University of Cincinnati, Cincinnati, Ohio.

Lepidostrobus aristatus, the original name of this species, was found to be preoccupied. Hoskins and Cross ('43b) proposed the name *Lepidostrobus arrectus*. The name refers to the condition of the attenuated laminae, which overlap, but are not closely appressed and arise at angles of 70 ° to 80° from the pedicels.

LEPIDOSTROBUS BARTLETTI Arnold, in Amer. Jour. Bot. 17:1028–1032, *figs. 1–3*. 1930.

Cone.—Entire, 2.5 × 11.5 cm., tapering gradually at both ends.

Axis.—Stele 0.5 mm. in diameter, central pith region surrounded by scalariform tracheids. All cortical tissue decayed.

Sporophylls.—Arranged spirally; pedicel about 1 cm. in length, borne at right angles to axis; lamina slightly more than 1 cm. long.

Ligule.—None observed.

Sporangia.—Dehisced and poorly preserved; approximately 5 mm. long and 2–3 mm. high; sterile plates of tissue extending into sporangial cavity.

Spores.—Scattered, not found in sporangia; microspores about 20 μ in diameter; megaspores broadly oval, 735 μ along largest diameter.

Locality and Horizon.—Shale pit one mile west of Grand Ledge, Michigan. Horizon listed as Pottsville.

Material.—Five ground sections and fragment catalogued as no. 12862 in Museum of Paleontology, University of Michigan, Ann Arbor, Michigan.

Only ground sections of the megaspores were available. The ridges on the spore wall indicate flanges or ear-like lobes similar to *Triletes* which Schopf ('38b) assigned to the section Auriculati. However, Dijkstra ('46) placed such spores in the Aphanozonati.

Lepidostrobus braidwoodensis Arnold, in Amer. Midl. Nat. 20:709–712. 1938.

Cone.—Incomplete, 35 mm. long, 14 mm. wide; compressed in nodule.

Axis.—No structural details preserved.

Sporophylls.—No structural details preserved.

Ligule.—None observed.

Spores.—One large and 3 aborted megaspores in each megasporangium; axial diameter of large spore exceeds 2 mm., of smaller spores less than 0.5 mm. Granular exine with small spinose appendages. No microspores present.

Locality and Horizon.—Strip mine dump between Braidwood and Coal City, Illinois. Carbondale (Allegheny) age.

Material.—Single specimen in Museum of Paleontology, University of Michigan, Ann Arbor, Michigan.

Arnold ('50) identified the large spore as *Lagenicula saccata,* and, although similar to *Cystosporites giganteus,* it differs in its conspicuous apical prominence and the granular spore wall (fibrous in *Cystosporites*).

Lepidostrobus coulteri (Coult. & Land) Jongmans, Foss. Cat. 2: pars 16. 1930; Mathews, in Bot. Gaz. 102:26–35, *figs. 1–2.* 1940.

Lepidostrobus Coult. & Land, in Bot. Gaz. 51:449–453, *pls. 28, 29, figs. 21–23.* 1911.
Lepidostrobus Coult. & Land, in Bot. Gaz. 72:106–108. 1921.

Cone.—Large, 5–6 cm. in diameter, up to 22 cm. long; all specimens incomplete.

Axis.—Tapering slightly, 8–9 mm. in diameter; stele 2.26 mm. in diameter with central tissue undifferentiated; xylem 400–500 μ thick; sporophyll trace collateral, attaining diameter of 400–600 μ in middle cortex.

Sporophylls.—Arranged spirally; pedicel 20 mm. long; lamina 20 mm. long, tapering; prominent heel about 3 mm. long. Parichnos strand accompanying sporophyll trace and bifurcating in pedicel.

Ligule.—Small and between distal end of sporangium and lamina base; sporophyll cells below ligular pit longer than other cells and radiating from pit.

Sporangia.—Attachment entire length of pedicel, 17 mm. long, 2.5–3 mm. broad. Small subarchesporial pad present but no radiating sterile tracts within sporangium. Palisade cells of wall about 75 μ high, attaining 125 μ at corners and decreasing to 25 μ at point of dehiscence.

Spores.—Scarce, scattered in dehisced sporangia. Only microspores present, 27 μ in diameter, frequently in tetrads about 50 μ in diameter.

Locality and Horizon.—Obtained from coal pocket in small drift mine near Indianola, Iowa. Horizon listed as Pottsville.

Material.—Sections G21, M1–M5 and G21, P1–P11. Botany Department, University of Chicago, Chicago, Illinois.

The specimens are preserved in calcium carbonate heavily impregnated with pyrite. Tilton ('12) reported *L. coulteri* to be the first description of a petrified *Lepidostrobus* from America.

LEPIDOSTROBUS GALLOWAYI Arnold, in Papers Mich. Acad. Sci. 17:51–56. 1932; in Amer. Jour. Bot. 22:23–25. 1935.

A lycopodiaceous strobilus . . . . Arnold, in Amer. Jour. Bot. 20:114–117, *figs. 1–7.* 1933.

Cone.—Specimen not petrified, partly preserved and enclosed in sandstone; attached to 3-inch peduncle 13 mm. in diameter. Strobilus 3.5 cm. in diameter by 10 cm. in length; apex bluntly rounded.

Axis.—Transverse sections not available.

Sporophylls.—Numerous, borne in whorls, 12–20 in a whorl, those in adjacent whorls alternating with whorls about 3⁄16 of an inch apart; 10–15 mm. long, borne at right angles to axis.

Ligule.—None visible.

Spores.—Arnold ('33) found microspores of two sizes, approximately 35 μ and 76 μ in diameter, and either smooth or slightly rough. He described the megaspore as about 150 μ in diameter, and with slender appendages. Preservation was so poor as to render assignment to any known group impossible, and even the size was approximate as no complete spores were obtained. More recent preparations[3] from the type have produced abundant microspores from the apex. These are clearly ***Plani-sporites*** Knox and quite similar to microspores of the same genus reported in ***Sigillariostrobus rhombibracteatus*** by Chaloner ('53c). They were 44–61 μ in diameter. Megaspores obtained from the base of the cone were numerous and differed greatly from the single one figured by Arnold ('33, fig. 2). None of them bore appendages, and although their condition was such as to prevent an accurate measurement, their diameter approximated 400 μ, considerably larger than the original diagnosis.

Locality and Horizon.—In quarry about 1½ miles northeast of Port Allegany, McKean County, Pennsylvania. Pocono Sandstone, lower Mississippian. It was difficult to assign a definite age to this cone because of uncertainty about the age of the horizon. Arnold described it as presumably upper Devonian on the basis of investigations up to that time. However, Wilmarth ('38), Weller et al. ('48), and Cooper ('42) have assigned the Pocono to the lower Mississippian.

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[3] The author is indebted to Dr. W. G. Chaloner for the spore preparations.

Material.—Single specimen in Museum of Paleontology, University of Michigan, Ann Arbor, Michigan.

Lepidostrobus Gallowayi is something of an enigma among lycopod cones. Originally, Arnold ('33) considered the possibility that it was sigillarian, largely on the basis of the whorled sporophylls. Although there is probably a greater tendency toward a verticillate arrangement in sigillarian strobili than in *Lepidostrobus,* the character has been reported often enough in *Lepidostrobus* to render it of little diagnostic value. Its heterosporous condition seemed to be sufficient grounds for Arnold's placing the cone in *Lepidostrobus.*

There is no satisfactory evidence for the existence of bisexual sigillarian cones. Leclercq ('38) did assign a bisporangiate cone to *Sigillariostrobus,* but Chaloner ('53b) found evidence of contamination in her specimen and indications that the microspores were not the original contents of the cone. He subsequently assigned the cone to *Lepidostrobus dubius.* The small megaspores of *L. Gallowayi* do not suggest sigillarian affinity, and the Aphanozonati megaspores which appear to characterize the sigillarians approximate 2 mm. in diameter, appreciably larger than even the largest spores obtained from *L. Gallowayi.*

Lepidostrobus Gallowayi possesses a peduncle about 3 inches in length. Arnold ('33) did not figure it, but an examination of the type specimen has left no choice but to consider it structurally a peduncle. The sporophylls and even the delicate lamina are preserved on all parts of the strobilus, but there is no evidence of appendages ever having been borne on the peduncle. Of course, in the absence of additional specimens, the possibility that the pedunculate stalk is a result of preservation, such as partial defoliation of the cone, must be considered.

The presence of this peduncle-like structure on a cone, which seems to be *Lepidostrobus* on the basis of bisexuality, is important because the manner in which the cones are borne on the plant has been considered a major character. Schopf ('41b) considered, and with good evidence, that *Lepidostrobus* was distinguished from sigillarian cones by the terminal attachment of *Lepidostrobus* to ordinary leafy twigs, whereas the latter were borne on specialized peduncles.

The presence of *Plani-sporites* cannot be regarded as conclusive evidence of sigillarian affinities despite the fact that this spore has been obtained from *Sigillariostrobus rhombibracteatus* Kidston (Chaloner, '53c) and occurred in *Mazocarpon oedipternum* Schopf.

From our knowledge of the spores of *Lepidostrobus* a close relationship seems to exist between this genus and the spore-form genus *Lycospora.* The essential feature of the former is a usually well-developed equatorial ridge, and a size range usually between 18 and 45 μ (Kosanke, '50), although Somers ('52) has reported it with a diameter of 50 μ. Microspores obtained from some species of *Lepidostrobus* have the ridge rather poorly developed (Chaloner, '53b), and it seems that there is a gradient from *Lycospora* to *Plani-sporites* in *Lepidostrobus;* the latter spore differs from *Lycospora* in the absence of an equatorial ridge and a greater size range, 25–130 μ in diameter. Thus, on the basis of these characters, the microspores of *L. Gallowayi* must be assigned to *Plani-sporites*, but the fact that there is a range from typical *Lycospora* to *Plani-sporites* does not permit the definite attribution of either spore to a single cone genus.

It would appear that this cone has definite sigillarian affinities and that Arnold was correct in his original diagnosis, but in the face of rather conclusive evidence against bisexuality in sigillarian cones, assignment to this group must be refrained from. If additional specimens prove to be pedunculate or if its vegetative correlative proves not to be *Lepidodendron*, its generic segregation from *Lepidostrobus* would be advisable.

LEPIDOSTROBUS IMBRICATUS Hoskins & Cross, in Amer. Midl. Nat. 24:427, *figs. 1–2, 5–11.* 1940; *ibid.* 29:541, *figs. 1–2.* 1943.

Cone.—Medium-sized, 1.8–2.5 cm. in diameter, over 13.5 cm. long, tip slightly tapered and bluntly conical. Preserved as sandstone cast.

Axis.—Approximately 4–5 mm. in diameter at base, tapering abruptly to 2–3 mm.; 13 sporophyll bases prominent in cross-section. No cellular detail observed.

Sporophylls.—Arranged spirally on axis with approximately 100 revolutions in 13.5 cm.; pedicels inserted at right angles to axis and about 8 mm. long to distal end where lamina curves evenly upward; no heel evident; lamina 1.5–2.0 cm. long, slender, not over 1.5 mm. wide at base, tapering gradually to sharp point, closely appressed, overlapping many laminae above, imbricate in appearance; median nerve prominent.

Ligule.—Definite evidence lacking, possibly due to imperfect preservation.

Sporangia.—Borne adaxially on pedicel, 6–8 mm. long and greatly elongated, wedge-shaped in top view and in cross-section near axis but broadly flattened at distal end and overlapping narrower sporophyll; attachment not distinguishable. Densely crowded vertically and laterally and distorted.

Spores.—Small, 26.5 μ in diameter, triradiate openings present in some; no larger spores found in cone.

Locality and Horizon.—Pocahontas sandstone, lower Pottsville series, Pennsylvanian system. Six miles northwest of Orleans, Orange County, Indiana; Chailleaux quarries.

Material.—Three specimens, one a fairly complete cone, are in the Paleobotanical Museum, Botany Department, University of Cincinnati, Cincinnati, Ohio. B-620, holotype; B-621, 622, 623, paratypes; B-1981, hypotype.

LEPIDOSTROBUS KENTUCKIENSIS Scott & Jeffrey, Scott in Roy. Soc. London, Proc. B 88:435–436. 1915; Scott, Stud. Foss. Bot. 2:159, 3d ed. 1920; Read & Campb. in Amer. Midl. Nat. 21:436, 439, 441. 1939; Hoskins & Cross, in The Paleobotanist 1:233. 1952; Cross & Hosk. in Compt. Rend. Trois. Cong. Strat. et Géol. du Carbonifère, Heerlen 1:116, 120. 1952.

Lepidostrobus Fischeri Scott & Jeffrey, in Roy. Soc. London, Phil. Trans. B205:355, *pl. 29, figs. 15–21; pl. 39, figs. 20–23.* 1914; Hirmer, Handb. d. Paleobot. 1:230. 1927.

Cone.—Large, 4 cm. in diameter by 8.5 cm. long. Incomplete, both ends missing but some tapering towards apex; preserved as weathered petrified fragment, largely of calcium phosphate and ferric carbonate.

Axis.—Approximately 7.5 mm. in diameter; stele about 1.65 mm. in diameter; central pith zone composed of xylem-like cells, but without scalariform markings, surrounded by narrow ring of exarch xylem with corona points corresponding to leaf traces; leaf traces mesarch with sheath of elongate cells, sheaths of adjacent traces confluent around stele; inner cortex 0.25 mm. thick with interwoven structure, but without gaps; outer cortex about 2.25 mm. thick, of narrow prosenchymatous elements, no clear distinction into middle and outer cortex.

Sporophylls.—Pedicels triangular in tangential view, minimum width near axis 1.5 mm., maximum width about 2.8 mm., 2 mm. high, upper surface with groove and median ridge; pedicels inclined downward from cone apex; vascular bundle (rarely preserved) lying in soft tissue above median ridge. Laminae not preserved.

Ligule.—Not observed.

Sporangia.—Borne adaxially on sporophylls, 17 mm. long and about 2 mm. high; palisade wall 120–180 μ thick; evidence of subarchesporial pad.

Spores.—Only microspores present, 48 × 60 μ in diameter; tetrads about 96 μ in diameter.

Locality and Horizon.—Described by Scott and Jeffrey as from one mile west of Junction City in Boyle County, Kentucky, and from a nodule layer 20–24 inches thick at the base of the Waverly (lower Carboniferous) and immediately above the Genesee Black shale (upper Devonian). This flora has been considered a Devonian one, but recent extensive study of the plants of the upper New Albany shale by Cross and Hoskins ('52) and Hoskins and Cross ('52) indicates it to be of lower Mississippian age.

Material.—Single specimen. Placed in collection of D. H. Scott, East Oakley House, Basingstoke, England. Duplicate set to E. C. Jeffrey, Harvard University, Cambridge, Massachusetts. None of the type material was made available for this study. It was originally named *Lepidostrobus Fischeri* for Mr. Moritz Fischer, the collector, but the name was found to be preoccupied and Scott ('15) proposed *L. kentuckiensis* after the state in which it was found. Scott and Jeffrey considered *L. kentuckiensis* to belong to the same group of Lower Carboniferous cones as *L. Brownii,* differing from the latter primarily in the structure of the cortex. The central stelar tissue was regarded as undifferentiated xylem rather than typical pith and was similar to the central tissue of *L. Brownii.*

The presence of microspores only does not necessarily indicate homospory, for the basal portion of the cone, where megaspores would be expected, was missing. Only one small radial section, containing a few damaged microsporangia, was available for study, thus limiting conclusions as to heterospory.

LEPIDOSTROBUS NOEI Mathews, in Bot. Gaz. 102:35–48, *figs. 3–7.* 1940; Hoskins & Cross, in The Paleobotanist 1:233. 1952.

Cone.—Incomplete, ovoid; both ends missing from fragment 11 cm. long, varying in diameter from 5.5 cm. in lower part to 7 cm. in upper. Petrified in calcium phosphate nodule.

Axis.—Seven mm. in diameter throughout known length; stele 2 mm. in diameter with central tissue of undifferentiated xylem 300–400 μ wide; sporophyll trace collateral, 100 μ in diameter in axis, composed of more than 30 xylem elements.

Sporophylls.—Mathews gave the sporophyll arrangement as spiral with a 2:51 phyllotaxy, but this may be considered whorled as indicated by his fig. 3A (1940). Lowermost sporophyll 7 mm. long, uppermost 22 mm., inclined at 70° in lower cone, 80° in upper; heel absent; laminae 8 mm. broad, 14 mm. long.

Ligule.—Not observed.

Sporangia.—Attached adaxially along entire length of sporophyll, 20 mm. long, with short, unbranched sterile plates extending into sporangium.

Spores.—Megaspores numerous (several hundred per sporangium) in basal sporangia, smooth with triradiate ridges, 320–375 μ in diameter. Microspores in upper sporangia, 50 μ in diameter, frequently in tetrads 76 μ in diameter.

Locality and Horizon.—Vicinity of Paint Lick, near Cartersville, Garrard County, Kentucky. New Albany shale, lower Mississippian.

Material.—Sections and slides G22, M1–M33. Botany Department, University of Chicago, Chicago, Illinois.

Some uncertainty existed as to the correct age of *L. noei,* and Mathews listed it as either Ohio shale (upper Devonian) or New Providence shale (Mississippian). Hoskins and Cross ('52) appear to have definitely established the age as lower Mississippian. The original type, a "weathered-out" specimen, was considered by Mathews to be preserved in calcium carbonate, but Hoskins and Cross found the medium to be calcium phosphate and that the fossil was indistinguishable from phosphatized plant fossils of the New Albany shale. They are of the opinion that it weathered out of the Sanderson or Bedford formations.

Due to increased interest in lycopod spores, the megaspores were examined in greater detail. They were numerous but difficult to macerate intact from the calcium phosphate matrix. The size is somewhat larger than given in Mathew's original description, being 320–375 μ in diameter, occasionally attaining 400 μ, but still rather small for megaspores. The spores are spherical or nearly so (figs. 20–22), characteristically smooth in general appearance. Microscopic examination revealed large numbers of small granular bodies 6–10 μ in diameter on the spore surface (fig. 23); these occurred in moderate amounts on both distal and proximal surfaces, appearing most abundant along the sutures. The spore coat is about 11 μ thick. Trilete rays are short, 120–150 μ long. Suture lines are distinct, often with moderate lips about 8 μ wide. Arcuate ridges are not distinguishable.

The spores are assignable to *Triletes,* a genus with affinities to the free-sporing lycopods. To the author's knowledge, *L. noei* has not been described as a free-sporing species.

GENERAL CONSIDERATION OF MORPHOLOGY AND EVOLUTION

The Ligule in Lepidostrobus.—A ligule was not observed in *L. pulvinatus* or *L. diversus,* and material of *L. diversus* was sufficiently well-preserved and abundant that the failure to locate the structure was somewhat unexpected. Its absence warrants re-examination of the evidence for ligulate members of the lepidostrobi. Although the ligulate character of *Lepidostrobus* is a generally accepted fact, there are relatively few instances of the positive occurrence of a ligule in the genus. Solms-Laubach ('91) apparently was the first to suspect its existence, his assumption being based on a probable ligular pit scar on lepidostrobi compression material. The first authentic report of the ligule was by Maslen ('98) in slides of *Lepidostrobus oldhamius* preserved in the Williamson collection. A ligular chamber was absent, but a ligule of some 0.5 mm. in length was overarched by the distal end of the sporangium. There was no evidence of tracheids or transfusion tissue in the ligule or between it and the vascular bundle of the sporophyll. There is reason to believe, however, that *L. oldhamius* is actually the microsporangiate cone of *Lepidocarpon* and was borne on *Lepidophloios.* Schopf ('41a) suggested a possible correlation of lepidocarp genera with *Lepidophloios* and also cited statements of Hemingway's to this effect.

There are reports of ligules in specimens definitely assignable to *Lepidostrobus. L. Veltheimianus* Sternberg (= *L. Scottii* Jongm.) is one of the better known and is represented in many text-books. Arber ('14) observed several examples in her anatomical study of the genus. Six ligules were figured from an apical section of *L. oldhamius* f. *pilosus.* She reported a ligular pit in several instances in *L. Binneyanus,* but a definite ligule was not evident. In *L. gracilis* Arber (= *L. Arberi* Jongm.) she described a ligule which was sunken in a pit.

Ligules have been reported in *Lepidostrobus Brownii,* the bisexual character of which seems sufficient grounds for lepidostroboid affinity. Zeiller ('09) observed a ligule at the cone's apex, along with a rudimentary sporangium. A ligule was also seen on a lower sporophyll bearing a mature sporangium.

Difficulty encountered in locating ligules may be partially explained by Zeiller's ('14) later work on the species. Several ligules were observed near the cone's apex and borne on the ventral surface of sporophylls in the manner of the ligule of *L. oldhamius.* In mature portions tissue of the ventral sporophyll completely decomposed in the ligular region. Zeiller considered the ligule to be ephemeral, atrophying, and decomposing rapidly. Well-preserved apices of *L. diversus* were available to this writer but showed no evidence of ephemeral ligules.

The existence of an eligulate heterosporous member of the Lycopodiales has never been satisfactorily demonstrated. Walton ('31) urged caution in attempting to establish the existence of eligulate heterosporous Lycopodiales, and he attributed the absence of a ligule in several members to leaf abscission in the region between the ligular pit and stem or to overlapping leaves in foliage-bearing specimens. In known ligulate Lycopodiales no evidence of a ligule remains when the sporophyll falls. Bode ('29) reported a cone genus *Porostrobus* from paper coals of the Moscow Basin as being eligulate and heterosporous. However, the plant to which he referred *Porostrobus* was demonstrated later by Wilson ('31) to be *Bothrodendron* and ligulate. Bode's interpretation of heterospory was also questioned by Walton ('31) who believed that two size ranges of megaspores were represented, as has been reported in *Mazocarpon shorense* Benson.

Of the ten species of American *Lepidostrobus* treated in this paper only one, *L. coulteri,* possessed a ligule, and its authenticity can be questioned because of the probability of its belonging to the Lepidocarpaceae. On the basis of available evidence it appears there is no indication that a ligule is a constant feature of the genus.

Cone Correlations.—Organic connection is the only reliable means of definite correlation of plant remains. Upon the establishment of a correlation detached specimens may be assigned to parent genera, providing dependable and constant characteristics of identification are present in both specimens. Even though relatively few known species of *Lepidostrobus* have been correlated with *Lepidodendron,* these have been numerous enough to demonstrate affinities of the two, and in *Lepidostrobus* there are examples of attached strobili well enough preserved to permit establishment of dependable characteristics. Consequently, some detached strobili can be accepted as valid representatives of the genus in that they possess distinct characters of those that have been found attached to *Lepidodendron* (i.e. *L. dubius*).

Megaspores are being increasingly used to determine lycopod cone species. Chaloner ('53b) found them to be the only diagnostic character of *Lepidostrobus dubius, L. allantonensis,* and *L. russelianus.* The appearance of *Triletes rugosus* in *L. diversus* reflects some doubt on the reliability of such identification alone, for this megaspore has been reported as occurring in *Lepidostrobus russelianus* and *L. olryi* (Chaloner, '53b), and Arnold ('49) figured a cone bearing the same spore. Actually there has been little effort previously to establish a correlation between megaspores and the fructifications which bore them and in turn to attribute the cone to a parent tree. It has only been recently that the value of macerations has been recognized in such correlative efforts, and many early spore preparations exist only as ground, non-serial sections.

Table III lists several megaspore species which have been correlated with lepidostrobi. However, actual instances in which known cone species have been associated with their vegetative correlatives are very few. Among the more reliable are *Lepidostrobus dubius* which has been found in organic connection with *Lepidodendron simile. Lepidostrobus russelianus* has been associated with *Lepidodendron acutum* Presl (*sensu* Nemejc). *Lepidostrobus olryi* was probably borne on a lepidodendroid parent plant, but there is some evidence that the parent plant might have been a *Bothrodendron.* The well-known *Lepidostrobus Veltheimianus* Sternberg (= *L. Scottii* Jongm.) has long been considered to be the fructification of *Lepidodendron Veltheimianum* (Kidston, '01, p. 61), but apparently this attribution was based on association only. Calder ('33) has linked *Lepidostrobus Brownii* with *Lepidodendron Brownii* Unger on similarity of anatomical features. However, proof of organic connection is lacking and such comparisons based on evidence of comparative structures is always rather questionable.

TABLE III

A CORRELATION OF MEGASPORE SPECIES WITH *LEPIDOSTROBUS*

Cone species	Spore	Authority
Lepidostrobus allantonensis	*Triletes crassiaculeatus*	Chaloner ('53b)
Lepidostrobus braidwoodensis	*Lagenicula saccata*	Arnold ('38)
Lepidostrobus diversus	*Triletes rugosus*	Felix
Lepidostrobus dubius	*Triletes horridus*	Chaloner ('53b)
Lepidostrobus Masleni	*Triletes diabolicus*	R. Scott ('06)
Lepidostrobus olryi	*Triletes rugosus*	Chaloner ('53b)
Lepidostrobus russelianus	*Triletes rugosus*	Chaloner ('53b)
Lepidostrobus zea	*Triletes auritus*	Chaloner ('53a)
**Lepidostrobus* sp.	*Lagenicula rugosa*	Arnold ('49, '50)

* Assigned to *Lepidostrobus russelianus* by Chaloner ('53b).

Lepidostrobus Jacksoni Arber was attributed to *Lepidodendron obovatum* Sternberg by Arber ('16), but the leafy shoot figured was probably too poorly preserved to justify definite assignment. It is noteworthy that in nearly every instance where cones have been reliably associated with *Lepidodendron,* their megaspores belong to the section Lagenicula of *Triletes,* and no strobilus bearing Lagenicula megaspores has been assigned to any genus except *Lepidodendron.* An exception is *Lepidostrobus zea* (Chaloner, '53a) bearing the megaspore *Triletes auritus,* which is assignable to the section Auriculata. However, on the basis of anatomical and microspore differences, *L. zea* might well deserve different generic status, and there is no evidence that it was borne on *Lepidodendron.*

Dioecioism in Lepidostrobus.—Available evidence indicates that cones of *Lepidocarpon, Mazocarpon,* and *Sigillariostrobus* were unisexual. Several species of *Lepidostrobus* with bisexual cones are known, and there is a possibility that all valid species of the genus may be bisexual, but such an assumption cannot be made without an explanation for several unisexual strobili attributed to the genus.

One of the best-known species of the genus is *L. oldhamius* Williamson which was treated by Maslen ('99) in a classic work usually regarded as the most complete account of the anatomy of these cones. The species is considered to be homosporous, possessing only microspores, but its homospory is debatable due to the fragmentary nature of Maslen's material. Several forms of the species were set up in his study, and in only one was there as many as two sections from the same specimen. From the large number of slides examined from various localities, megasporangia should have been evident if present. Many additional specimens have since been studied without the discovery of a bisexual cone. The possibility, mentioned previously, of *L. oldhamius* being a lepidocarp fructification could explain the absence of a bisexual cone.

On the basis of Williamson's ('93) microsporangiate cone, *Lepidostrobus foliaceous* Maslen (= *L. Masleni* Jongm.) had been considered unisexual. However, R. Scott ('06) found a megaspore, tentatively named *Triletes diabolicus,* in Williamson's type cone as well as in the majority of specimens of this species in Scott's collection. The spore's morphology is still undetermined since macerations are evidently unavailable. The same species was considered by Campos ('25) to be a principal piece of evidence for homospory in *Lepidostrobus.* He possessed a splendid specimen from the Halifax Hard Bed of Huddersfield, Yorkshire, England, which he believed represented the entire cone and he was convinced it contained only microspores. The cone was only 5.1 cm. long, and its average diameter was 2.4 cm., indicating a stubby, ovoid strobilus. Twelve transverse ground sections were made, and it is probable, judging from Campos' description, that he never saw the specimen before preparation. A study of the twelve sections shows that the apex (G1-8) is undoubtedly present, and preservation is so excellent as to leave no doubt but all the sporangia contain microspores. However, Campos based his belief that he possessed the entire cone upon evidence provided by the two lowermost sections (G6-18, 19). They were considered basal because of a converging of the general outline toward the base, the total absence of sporophyll lamina sections on the two lowest slides, and the decreased number of sporangia sections. If truly basal, there could have been no megasporangia present.

An examination of the slides indicated that there is not a converging of sporangia but rather a distortion of arrangement as if by pressure. In upper sections there is a uniform arrangement of numerous stalked pedicels about the axis; this is peculiar to the species due to the oblique angle at which the pedicel departs from the cone axis. In sections G6-18, 19 the arrangement has been lost and the pedicels pushed to one side. In upper sections very few sporangia are distorted and there is little evidence of dehiscence, but basal sporangia are considerably disarranged and broken. As for the total absence of sporophyll lamina, *there are several lamina in the two lowest slides.* Most of them are broken and pushed to one side but are easily recognized by the indiscriminately scattered cells with dark contents (or secretory sacs), which were mentioned as characteristic of the species by Maslen ('99). It is very possible that the base of the cone is missing and subsequently the megaspore region also.

In an emended diagnosis of *Lepidostrobus dubius* Binney, Chaloner ('53b) describes cones containing megasporangia throughout or megasporangia in the basal part and microsporangia at the apex. Inasmuch as the spores in both belonged to *Triletes horridus,* two names of *forma* status were used to distinguish two types of cones. *L. dubius* forma *megalophorus* contained only megaspores, which occupied the cone to the apex. *L. dubius* forma *hermaphroditus* contained megaspores at the base and microspores at the apex.

It has been acknowledged that dioecioism probably existed in lepidostrobi, and *L. dubius* forma *megalophorus* doubtless represents an authentic example.[4]. It is also possible that *L. Masleni* of Campos ('25) was microsporangiate, but characteristics of the genus; particularly those species whose vegetative correlatives have been ascertained, indicate that *Lepidostrobus* consists of bisexual cones.

It is notable that this odd distribution of sporangia may be found in *Selaginella.* Sykes and Stiles ('10) found microsporangia to be rare in *Selaginella Vögelii.* In some cones only one mature microsporangium would occur in association with numerous megasporangia, and occasionally only megasporangia were present in a cone. In her extensive treatment of *Selaginella,* Mitchell ('10) listed four types of sporangial distribution: 1, a single large basal megasporangium, the other sporangia being microsporangia; 2, several basal megasporangia, followed by apical microsporangia; 3, cones wholly megasporangiate or microsporangiate; 4, an indiscriminate arrangement of mega- and microsporangia.

Basically, it appears that *Lepidostrobus* was bisexual, but there is no valid reason why dioecioism could not also have occurred. Examples of irregular spore distribution, such as occurs in *Selaginella* (Duerden, '29), have been recorded among fossil lycopods, and the variation in extant lycopod sporangia arrangement suggests the multitude of possibilities in strobili of this genus which was at the peak of evolvement during the Carboniferous.

That such digressions from normal sporangial development do occur in fossil species has been shown by Bocheński ('36) in *Lepidostrobus major;* normally there were one large and three abortive megaspores but there were frequent instances of abnormal spore development consisting of one normal and one abortive, one normal and two abortive, and even one large and 15 degenerated spores (Pl. V, figs. 31, 31a).

Sporophyll Arrangement.—The sporophyll arrangement of the lepidostrobi has lost significance as an important character. It was long considered to be spiral, and Bocheński ('36), among others, suggested the verticillate arrangement as a feature of *Sigillariostrobus.* Chaloner ('53b) found specimens of *Lepidostrobus russelianus* with a whorled arrangement and other specimens with a spiral phyllotaxy. Also, some specimens of *L. dubius* were discovered with whorled sporophylls although most specimens were spiral. Inasmuch as the vegetative correlative of both species

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[4] In an interview with Chaloner he told me that he was aware of the importance of this specimen and that great care had been taken to establish definitely its megasporangiate character.

is known to be *Lepidodendron,* both forms of phyllotaxis may occur in the same species.

Zeiller ('14) has reported a verticillate arrangement in *L. Brownii,* and the American species, *L. noei* and *L. Gallowayi,* have a similar phyllotaxy. It is probable that *L. Veltheimianus* Sternberg (= *L. Scottii* Jongm.) is another example of both arrangements occurring in a single species. Williamson ('72) described this species as spirally arranged, while Scott ('20) noted specimens with sporophylls in alternate whorls.

Evolution in Lepidostrobus.—Several workers have considered an evolutionary trend in the lepidostrobi which has led to *Lepidocarpon.* Bocheński ('36) considered *Lepidostrobus major* to be a connecting link to *Lepidocarpon Lomaxi* Scott[5] in a phylogenetic series to the Lepidocarpaceae. Similarily, Hirmer ('37) regarded *Lepidostrobus major* and *L. Bohdanowiczii* as forms transitional between the free-sporing lepidostrobi and *Lepidocarpon.*

Arnold ('38) suggested that the lageniculate *Triletes* represented a distinct evolutionary trend toward a reduction in megaspore number, with a corresponding increase in spore size; the height of the development was attained by *Lepidocarpon* where the single large megaspore was retained and protected by the integument-like outgrowth. He considered forms such as *L. braidwoodensis* as intermediate between many-spored forms and the *Lepidocarpon* type. It seems quite probable that such an evolutionary trend occurred, but it is unlikely that *Lepidocarpon* was the result. The stratigraphic range of *Lepidocarpon,* as given by Schopf ('41a), is comparable to that of *Lepidostrobus,* and it is well represented throughout most beds containing *Lepidostrobus.* It has been confirmed that *Lepidostrobus* was borne on *Lepidodendron,* while most evidence points to *Lepidocarpon* being the fructification of *Lepidophloios.* However, there is some question whether the leaf-cushion character of these genera are distinctions of generic importance.

Schopf ('41a) was of the opinion that the lepidocarps comprised a family group of natural affinities, and that the differences between the lepidocarp fructifications and those of the free-sporing lycopods were valid criteria for family differentiation. Thus, one of Scott's diagnostic characters, "the development of a single functional megaspore in each sporangium," is now found in two different genera. It would appear that this megaspore has not received the attention it deserves, and many workers have been over-eager to assign large sac-like megaspores to *Cystosporites.* Schopf's ('38b, p. 38) diagnosis of the genus included: "spore coat composed of interlocking matted fibrils, widely spaced and porous in the intermediate zone." He did associate it with the Lepidocarpaceae, though noting later ('41a, p. 555) that it might belong to the Lepidocarpaceae only in part.

In every instance where integumented Lepidocarpaceae *(Lepidocarpon, Illiniocarpon)* megaspores have been isolated they have shown the fibrous spore coat

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[5] Bocheński referred to a *Lepidostrobus Lomaxi* in his text (p. 211). However, there is no such species of *Lepidostrobus,* and *Lepidocarpon Lomaxi* was obviously intended.

(Darrah, '49). To this author's knowledge a fibrous-textured spore has never been isolated from unquestioned lepidostrobi. *Lagenicula saccata,* the single functional megaspore of *Lepidostrobus braidwoodensis,* most nearly approaches the lepidocarp character among the lepidostrobi. However, this spore is no larger than some species in which all the megaspores of a tetrad were functional; it possesses a granular extine (rather than fibrous) and the apical prominence characteristic of the section Lagenicula of *Triletes.*

It appears that distinction must be made between *Cystosporites* and those *Triletes* with a single functional megaspore per tetrad. There is no evidence that the lepidocarps contained any seed megaspore other than the fibrous-textured spore, *Cystosporites.* The only notable instance of its being reported in *Lepidostrobus* is by Bocheński ('36) in *L. major* and *L. Bohdanowiczii,* and it has been suggested that Bocheński's material may be referable to *Lepidocarpon* (Schopf, '38a, p. 143; '41a, p. 560). This is quite probable since Bocheński ('36, '39) mentioned *Cantheliophorus* (Bassler, '19) as representing the same type of fructification as *L. major* and *L. Bohdanowiczii,* while Schopf ('41a) noted that *Cantheliophorus* was actually *Lepidocarpon,* misinterpreted because of manner of preservation. Rather than a transition of forms from many-spored lepidostrobi to *Lepidocarpon,* structurally similar forms appear to have arisen independently and attained a comparable level of development.

Forms such as *Lepidostrobus braidwoodensis* seem most likely the developmental height of a *Lepidostrobus* line. That there will probably be additional examples of evolvement to a single functional megaspore is indicated by the recent discovery of *Lepidostrobus monospora* by Chaloner ('54). Its only significant difference from *L. braidwoodensis* is in the ornamentation of its large saccate spore. Both must be included in the lepidostrobi due to the absence of any integumentary organ and because of the granular texture of the spore coat.

Sigillarian Fructifications.—The cone genera *Mazocarpon* and *Sigillariostrobus* have been satisfactorily demonstrated to belong to *Sigillaria.* It has been suggested that the two genera are synonymous. Schopf ('41b) has recognized the evidence favoring such an interpretation, but he would keep them in different genera.

It seems likely that all sigillarian cones were unisexual. Schopf ('41b) discussed this problem fully, and his questioning of the authenticity of Leclercq's ('38) bisexual *Sigillariostrobus sphenophylloides* has proven justifiable by Chaloner's ('53b) assignment of the species to *Lepidostrobus dubius.* Bocheński ('39) has made probably the most comprehensive study of *Sigillariostrobus* in his treatment of S. *Czarnockii* Boch., S. *rhombibractiatus* Kidst., and S. *ciliatus* Kidst. He confirmed the pedunculate character of the genus, and all three species possessed unisexual cones, i.e., microsporangiate and megasporangiate.

Megaspores of cones reliably attributed to *Sigillaria* have been placed in the Aphanozonate section of *Triletes. T. glabratus* and *T. mamillarius* are the only two megaspores attributable to sigillarian cones; neither of these are known to occur in *Lepidostrobus*. Chaloner ('53c) also made the interesting observation that these sigillarian megaspores were more or less concave-convex or saucer-shaped and not spherical. This shape apparently stems from the large central mass of parenchymatous tissue of the *Mazocarpon* sporangium, a feature used to distinguish it from *Lepidostrobus*.

Schopf ('41b) found little specific difference between cones of *Lepidostrobus* and microsporangiate cones of *Mazocarpon oedipternum*. He considered the chief specific distinction to be the pedicel, that of *M. oedipternum* having broad lateral laminae and the pedicel of *Lepidostrobus* being quite contracted. Microspores of *M. oedipternum* are about 60 μ in diameter, significantly larger than those of *Lepidostrobus*. The pedunculate character separating the two has been dealt with previously.

The distinctive feature of *Mazocarpon*, its extraordinary development of intrasporangial tissue, is not characteristic of *Lepidocarpon* or *Lepidostrobus*, and it has been considered that this tissue is sufficient to distinguish microsporangiate cones of the three genera. Benson ('08) did figure a massive intrasporangial pad for microsporangia of *Mazocarpon pettycurense*, and in *M. shorense* (Benson, '18) the microspores were supposedly produced in pockets of massive intrasporangial tissue. However, in *M. oedipternum* there is no evidence of intrasporangial tissue in mature microsporangia such as occurred in the megasporangia, and the type slides showed no more sterile tissue than occurs in most lepidostrobi. Immature microsporangia at the cone's apex possessed a large subarchesporial pad, but a similar feature may be observed in most lepidostrobi.

The only reliable criteria at present available for distinguishing the microsporangiate cones from *Lepidostrobus* specimens possessing only microsporangiate features are the broad pedicel and characters of the microspores. The spores are assignable to *Plani-sporites*, but this form genus cannot be considered as conclusive evidence of sigillarian affinity. However, microspores of both *M. oedipternum* and *M. shorense* are far larger than any lepidostrobi microspores.

THE GENUS LEPIDOCARPON

The genus was established by Scott ('00) to include fossil seeds which Williamson ('77) had referred to Brongniart's genus *Cardiocarpon*. Scott's original diagnosis was based principally on the presence of microsporangia and megasporangia. Each was surrounded by an integument which completely enclosed the megasporangium except for a slit-like micropyle, and a single functional megaspore was contained in each megasporangium. In a revised diagnosis Scott ('01) omitted mention of the microsporangiate structure, which he had believed to be related to *Lepidocarpon* due to the presence of rudimentary integuments. Other inclusive generic descriptions have been made by Hoskins and Cross ('41) and Schopf ('41a).

Although many species of *Lepidocarpon* have been described in England and America, most workers have studiously avoided mention of a microsporangiate cone, preferring to use characters of the seed-like organ described by Scott. That such a microsporangiate strobilus was certainly present is evidenced by the absence of a heterosporous *Lepidocarpon* strobilus, although many magnificent specimens have been scrutinized for it. Andrews and Pannell ('42) described a microsporangiate strobilus for *Lepidocarpon magnificum.* Two strobili were found in close association to the seed-like organs. The principal evidence was the great abundance of microspores within the seeds, which are indistinguishable from those of the microsporangiate cones. It was noted, too, that not only were the microspores comparable in size and form but frequently occurred in tetrads in seeds as well as in microsporangia. The two cones revealed no evidence of an integument enclosing the sporangia, and are so typically lepidostroboid that if found alone, they would have almost certainly been classified as *Lepidostrobus.*

Scott considered the *Lepidocarpon* integument as a new organ arising from the superior face of the pedicel and not interpretable as an unfolding of lateral wings of the pedicel. Schopf ('38a) confirmed this interpretation in his treatment of *Lepidocarpon,* and in *Illiniocarpon* he reported the integument as further elaborated and entirely distinct from the sporophyll lamina. Hoskins and Cross ('41) have been the most recent dissenters of this theory and they considered the integument in *L. ioense* to be due to lateral development of the pedicel. However, disputed though its origin may be, this investing structure remains the best diagnostic criterion for the genus.

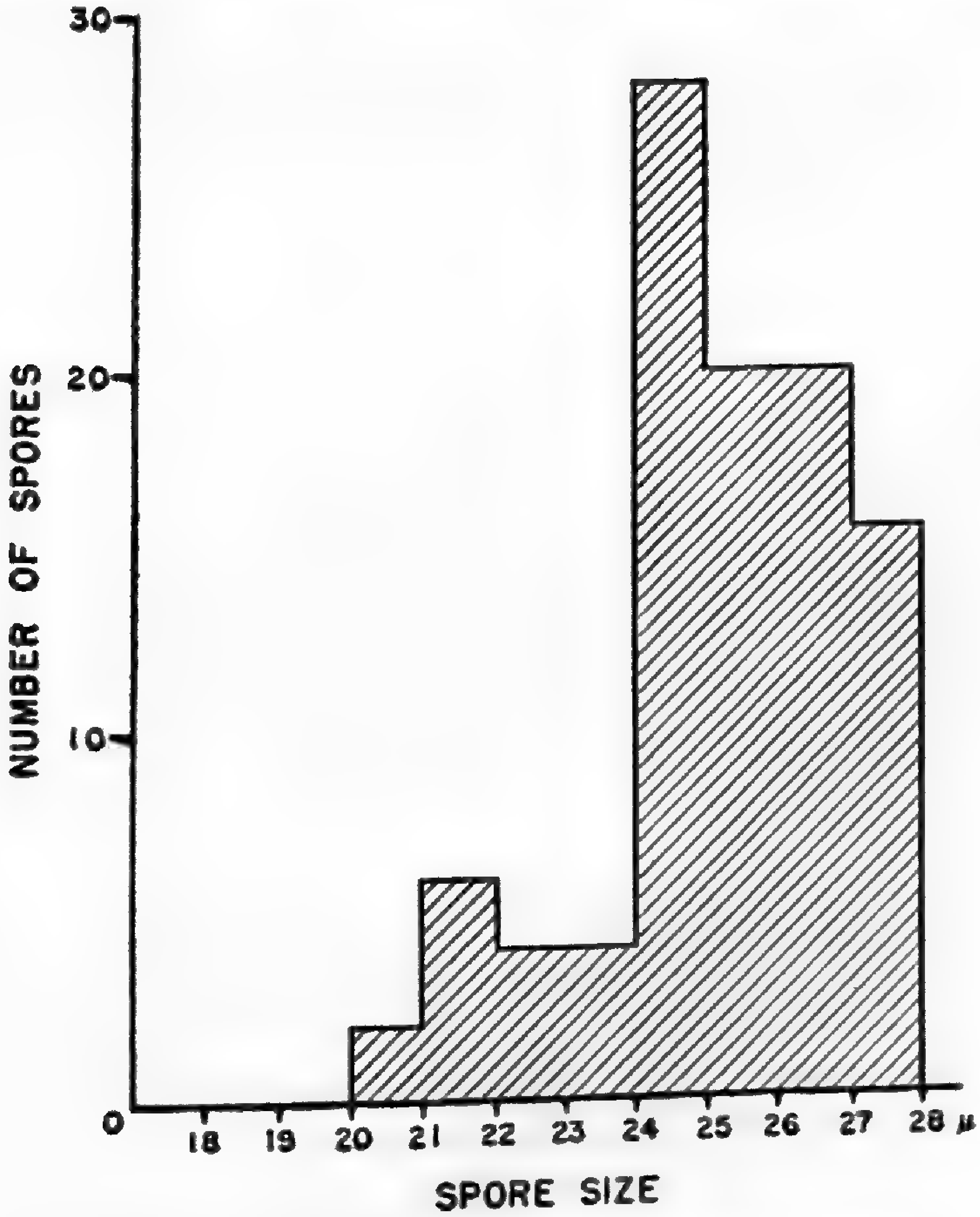
As noted previously, Schopf's ('41a) revised diagnosis featured the relatively enormous megaspore with its fibrous-textured coat. Assignable to *Cystosporites,* there is no question of a partial relationship between it and the Lepidocarpaceae. Since this spore has never been reliably assigned to *Lepidostrobus,* it assumes added significance when evidence of an integument is lacking, a frequent occurrence, particularly in compression material.

Andrews and Pannell ('42) give the microspores of *Lepidocarpon magnificum* as 26 μ in diameter, and the histogram (text-fig. 6) shows a range between 20 and 28 μ. Spores used were not in tetrads and were assumed to be mature on the basis of ornamentation, ray, and flange characters. The large numbers occurring in tetrads are characteristic of the species, and some difficulty was encountered in isolating sufficient mature spores for the diagnosis and histogram. All are attributable to *Lycospora* and are radial, trilete, and somewhat triangular in a transverse plane (figs. 46–48). The equatorial ridge is quite distinct. In width it averages 2.5 μ and occasionally reaches 3.5 μ, and the outer portion is clearly transparent. The rays are 9.6–11 μ long and extend to the equatorial ridge. The spore coat is punctate, the punctations being more pronounced than those of microspores of *Lepidostrobus diversus.* The spores are similar to *Lycospora punctata* (Kosanke, '50) and differ primarily in their much smaller size.

That species assigned to *Lepidostrobus* might be microsporangiate *Lepidocarpon* strobili was suggested by Andrews and Pannell in recognizing the close agreement between *Lepidostrobus coulteri* and *Lepidocarpon magnificum.* Arber ('14) had previously considered *Lepidostrobus oldhamius* as agreeing most closely with *L.*

coulteri. *L. coulteri* and the supposed microsporangiate cone of *Lepidocarpon magnificum* do agree so nearly in all dimensions as to render separation virtually impossible. The microspores are comparable in size, but few specimens of *L. coulteri* contained appreciable numbers of spores, and no macerations of these are available. Comparisons of spores from peels are not reliable and do not show critical features sufficiently well.

There are several specimens in the Washington University collection which are indistinguishable from *Lepidocarpon magnificum* and *Lepidostrobus coulteri*, although they are generally somewhat smaller. Specimens 846, 847, 848, 911, 912, and 918 are from the Booneville (Indiana) locality, and 924 is from Mineral, Kansas. Specimens 23 and 95, of the University of Illinois collection, are in coal balls from Nashville and New Delta, Illinois, respectively. In addition, the Booneville coal balls contained compressed masses of similar large axes and sporophylls intermingled with material of *Lepidostrobus diversus*. These cones attained a considerable length although none of them were complete. Specimen 911 was 9.2 cm. long, 912 over 20 cm., and 924 was 12.3 cm. long. These dimensions compare favorably with the 16 cm. recorded for *Lepidocarpon magnificum* and 22 cm. for *Lepidostrobus coulteri*. Table IV gives measurements of several of these specimens in which good transverse sections were available and affords a comparison with



Text-fig. 6. Histogram of microspore size in *Lepidocarpon magnificum* from a population of 100 mature spores. WCB 166.

L. magnificum and *L. coulteri.* Several of the cones contained microspores, all of them *Lycospora* and resembling rather closely the spores of *Lepidocarpon magnificum* in size range and other morphological features. Spores from specimen 847 are characteristic of those occurring in these cones (figs. 50–53), and tetrads occurred frequently as in *Lepidocarpon magnificum* (fig. 49).

TABLE IV
MEASUREMENTS OF ANATOMICAL COMPONENTS OF SEVERAL LYCOPOD CONES

Specimen	Stele diameter (mm.)	Xylem width (μ)	Cone diameter (cm.)	Axis diameter (mm.)	Pith diameter (mm.)	Horizon locality
Lepidostrobus coulteri	2.26	521.5	5–6	8–9	1.22	Pottsville Indianola, Iowa
Lepidocarpon magnificum	1.4	400	5.0	7.0	0.6	Illinois coal #6 Carbondale, Pennsylvanian Pinckneyville, Illinois
WCB 911	1.1 x 1.5	175	1.3 x 2.6	6 x 6.5	0.7 x 1.1	Petersburg coal #5 Des Moines, Pennsylvanian Booneville, Indiana
WCB 918	1.7 x 2.6	298	2.3 x 5.9	6 x 13	1.1 x 2	Petersburg coal #5 Des Moines, Pennsylvanian Booneville, Indiana
WCB 924	1.1 x 1.3	250	2.1 x 4	3.8 x 6.4	0.67 x 0.78	Fleming coal Des Moines, Pennsylvanian Mineral, Kansas
95a	1.6 x 1.7	230	2.6 x 3.2	6.2 x 6.6	0.92 x 1.8	Illinois coal #6 Carbondale, Pennsylvanian New Delta, Illinois

The reliability of microspores in specific determinations has not as yet been definitely ascertained. These spores are evidently *Lycospora* and within a similar size range but there is no conclusive proof for synonymy. The best positive evidence for synonymy in these cones appears to be the spores, but these are lacking or macerations are not available. Thus, on the basis of available data, it seems most expedient to leave *Lepidostrobus coulteri* in the lepidostrobi subject to further spore studies. The numerous strobili referred to above may be tentatively assigned to *Lepidocarpon,* although not necessarily to *L. magnificum.*

That some of these cones are probably the microsporangiate fructifications is suggested by the close association of several of them with a hitherto undescribed *Lepidocarpon.* Specimen 918 is an apparently microsporangiate cone with empty sporangia, and numerous *Lepidocarpon* seeds are preserved in association with it. Specimen 911 also lies close to many such structures, and it could well be the cone on which they were borne, for it consists of little more than an axis with several seeds in close proximity.

The *Lepidocarpon* seed organs which occur in considerable numbers and in close association with these cones are characteristic primarily because of the integumentary structure. And though other characters differ little from those of previously described *Lepidocarpon* species, none of the present descriptions are applicable to these specimens.

The seeds occur detached (fig. 55) and are approximately 10 mm. high in the central portion and 10.5 mm. wide at the broadest point. The cells of the sporangium wall are horizontally elongated. One functional megaspore occupies most of the sporangium; its walls are composed of the interwoven fibrils characteristic of *Cystosporites*. The investing integumented structure is distinguished by a dense covering of prominent protuberances which extend from the base to the micropylar slit (figs. 56, 57). The projections are 55–100 μ long and produce a crenate appearance.

LEPIDOCARPON **crenatum** Felix, sp. nov.

Detached seeds, approximately 10 mm. broad by 10 mm. high; one functional megaspore of the *Cystosporites* type occupying most of the sporangial cavity; investing integumental structure covered by small protuberances 55–100 μ long, giving a crenate appearance.

Locality and Horizon.—Strip mine near Booneville, Indiana; Petersburg V coal, Des Moines series, middle Pennsylvanian.

Type specimen.—WCB 816B, Washington University, St. Louis, Missouri.

Two specimens of interest were found in a coal ball of the Mineral (Kansas) locality, deposited in the University of Cincinnati collection (figs. 58, 59). To all appearances they were integumented lepidocarp sporangia containing microspores. The occurrence of such microsporangia would be most unlikely, and the only previous report of such a structure was by Scott ('00) and never actually confirmed. The integument wall of these seed-like organs was 200–215 μ thick and the columnar sporangial wall about 30 μ thick. Several hundred spore-like bodies were enclosed within each (fig. 54). They ranged from 45 to 60 μ in diameter, with walls about 2 μ thick. Peel sections did not show ornamentation or evidence of trilete rays, and numerous maceration attempts failed to isolate anything resembling spores.

That the bodies are not lycopod spores is further suggested by the presence of a prominent megaspore membrane 15–20 μ thick, which upon maceration showed the interlocking fibrils characteristic of *Cystosporites*. The spores are probably fungal, which would explain their poor preservation and also account for their lack of tetrad scars. The relative concentrations suggest an origin within the seed, and none were visible in the matrix external to the integuments. The possibility exists that they might be the functional equivalent of some extant smuts, which replace seed tissue with spores.

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Explanation of Plate

PLATE 13

Lepidostrobus diversus Felix

Fig. 1. Transverse section of cone through transition zone, showing single megasporangium in spiral of microsporangia. WCB 857 B/3, × 6.9.

Fig. 2. Slightly oblique longitudinal and transverse sections of transition zone, showing single megasporangium two spirals above one shown in fig. 1. WCB 857 A/5, × 5.6.

Fig. 3. Slightly oblique longitudinal and transverse sections of transition zone with three megasporangia visible. Basal megasporangium is single one visible in fig. 2. WCB 857 A/9, × 5.6.

Fig. 4. Oblique longitudinal section of transition zone. Two megasporangia visible are two upper ones of fig. 3, the basal megasporangium of fig. 3 having passed out of the plane of section. WCB 857 A/10, × 5.6.

Fig. 5. Oblique longitudinal section of transition zone, showing new megasporangia appearing on left and right sides of axis. Lower megasporangium on left side of axis is upper one of fig. 4, the lower one having passed out of the plane of section. WCB 857 A/20, × 5.6.

Fig. 6. Radial longitudinal section of sporophylls, showing lobed heel; sporangia have dehisced. WCB 897-1, × 11.2.


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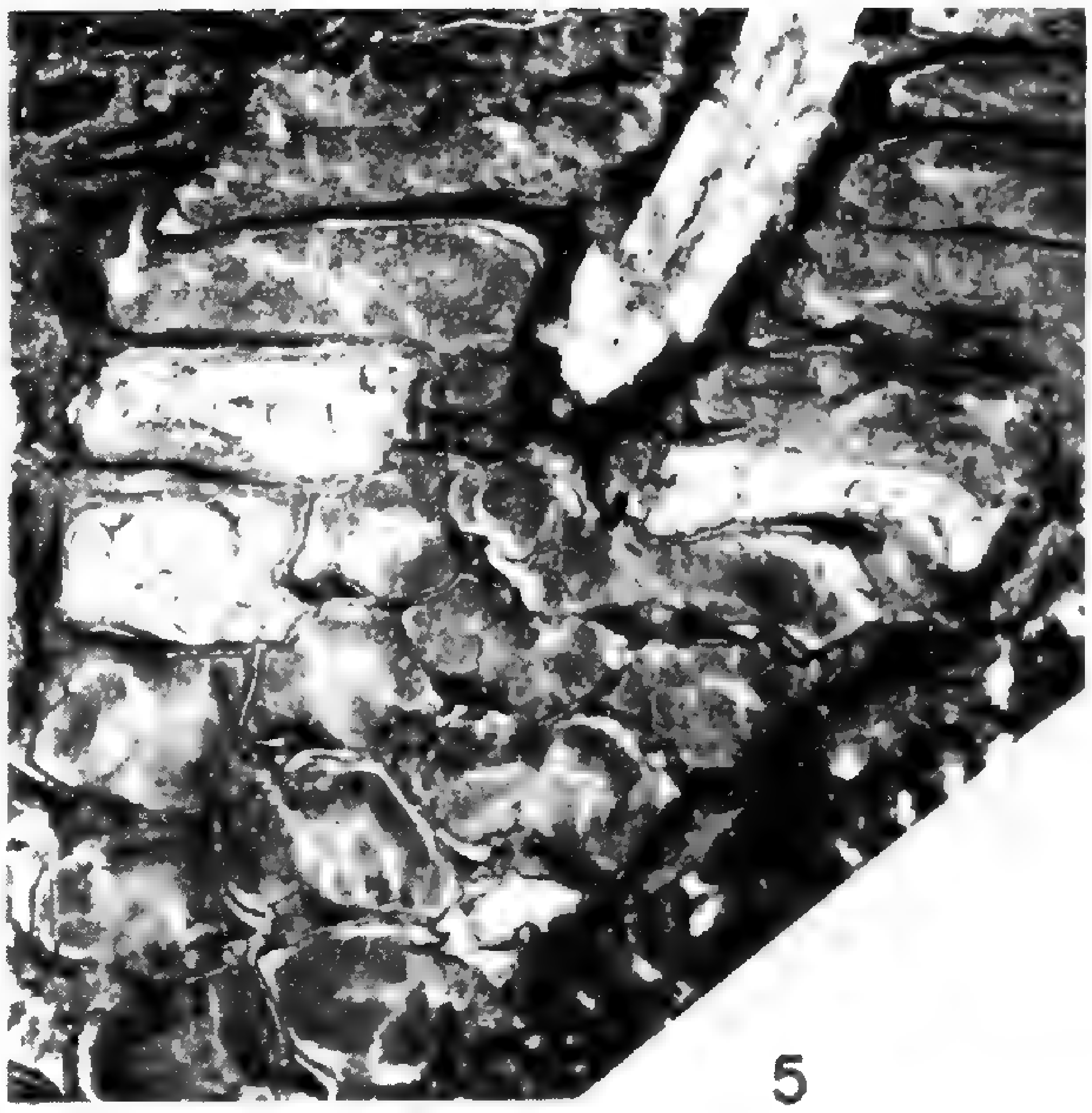
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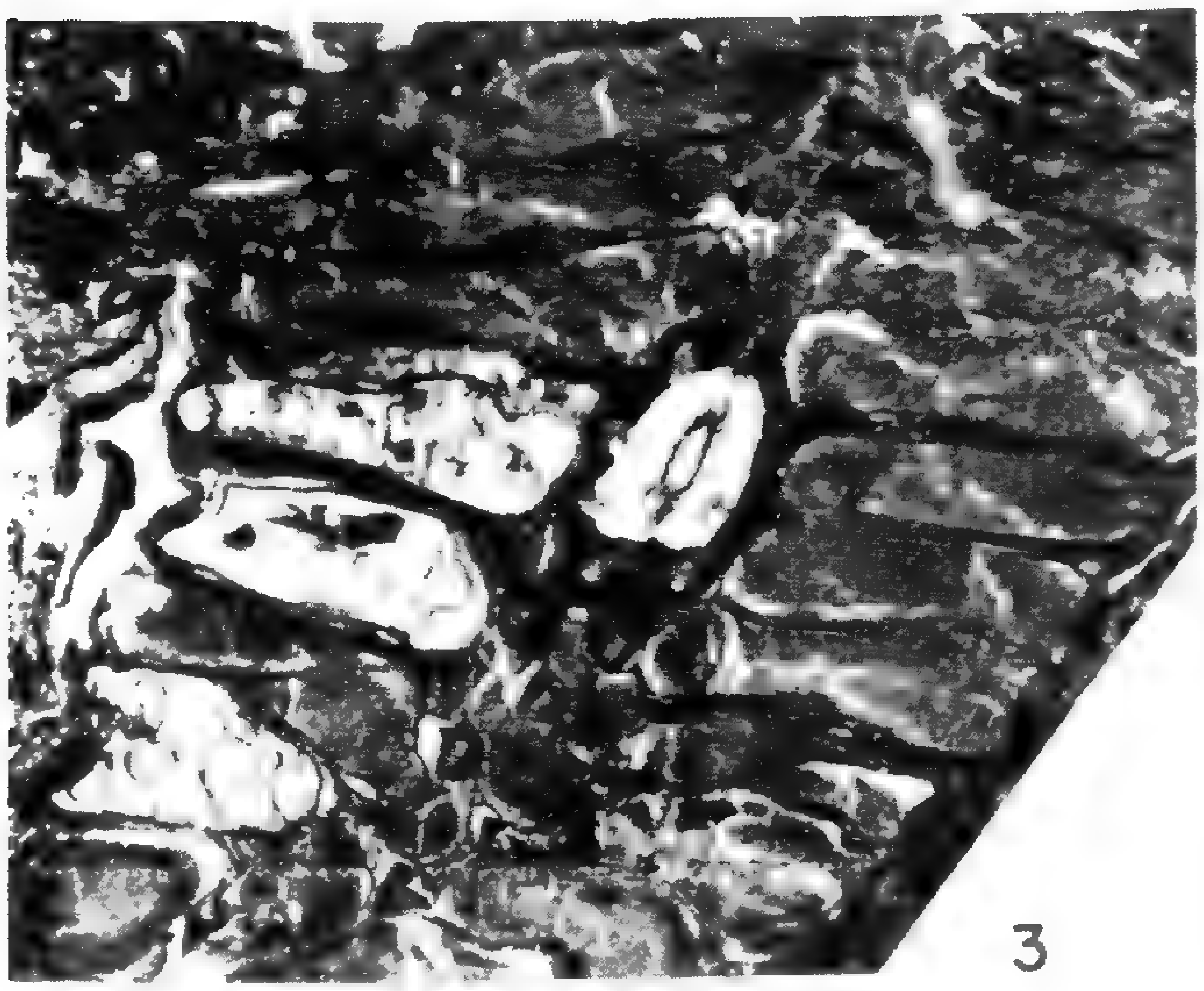
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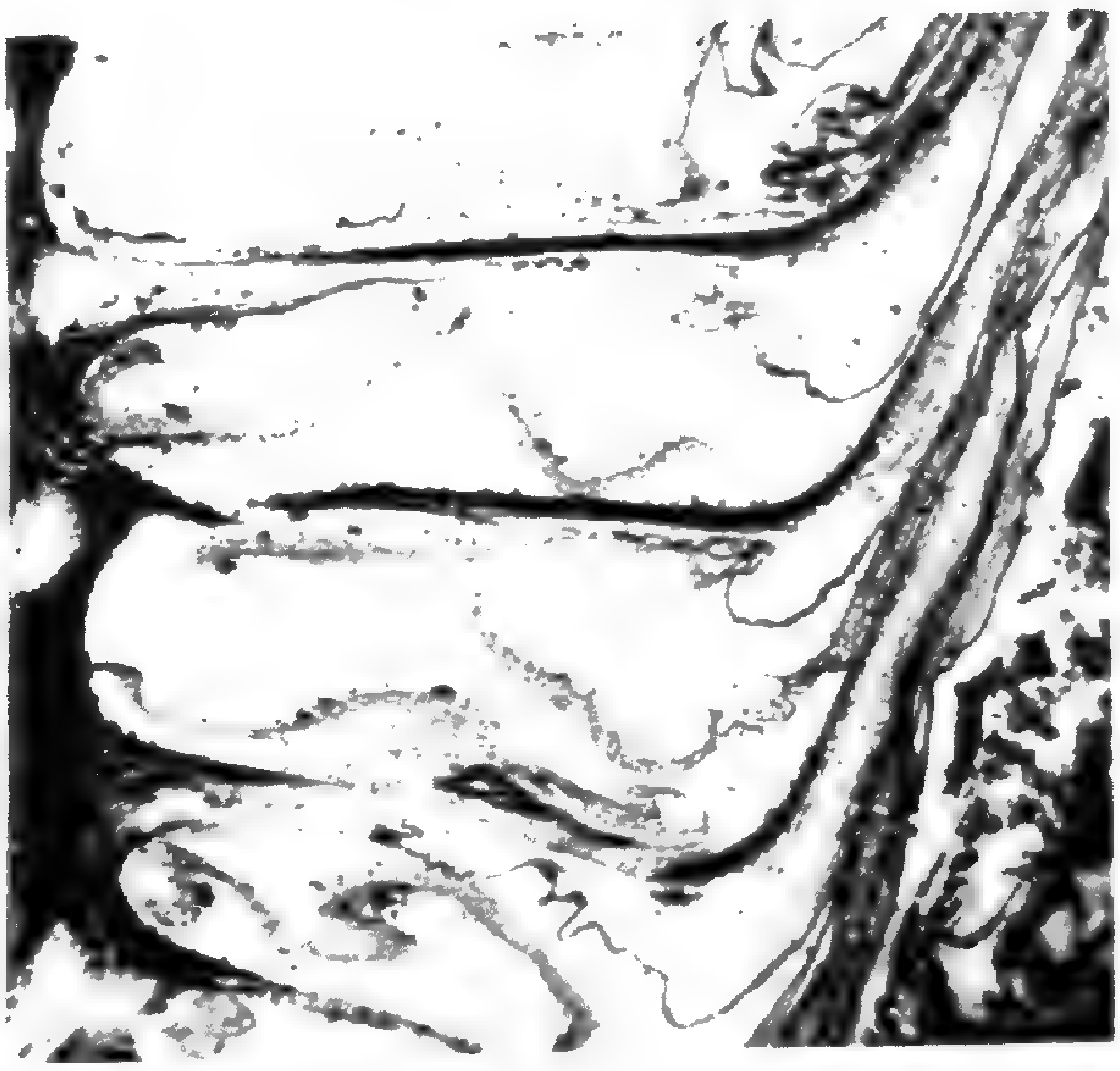

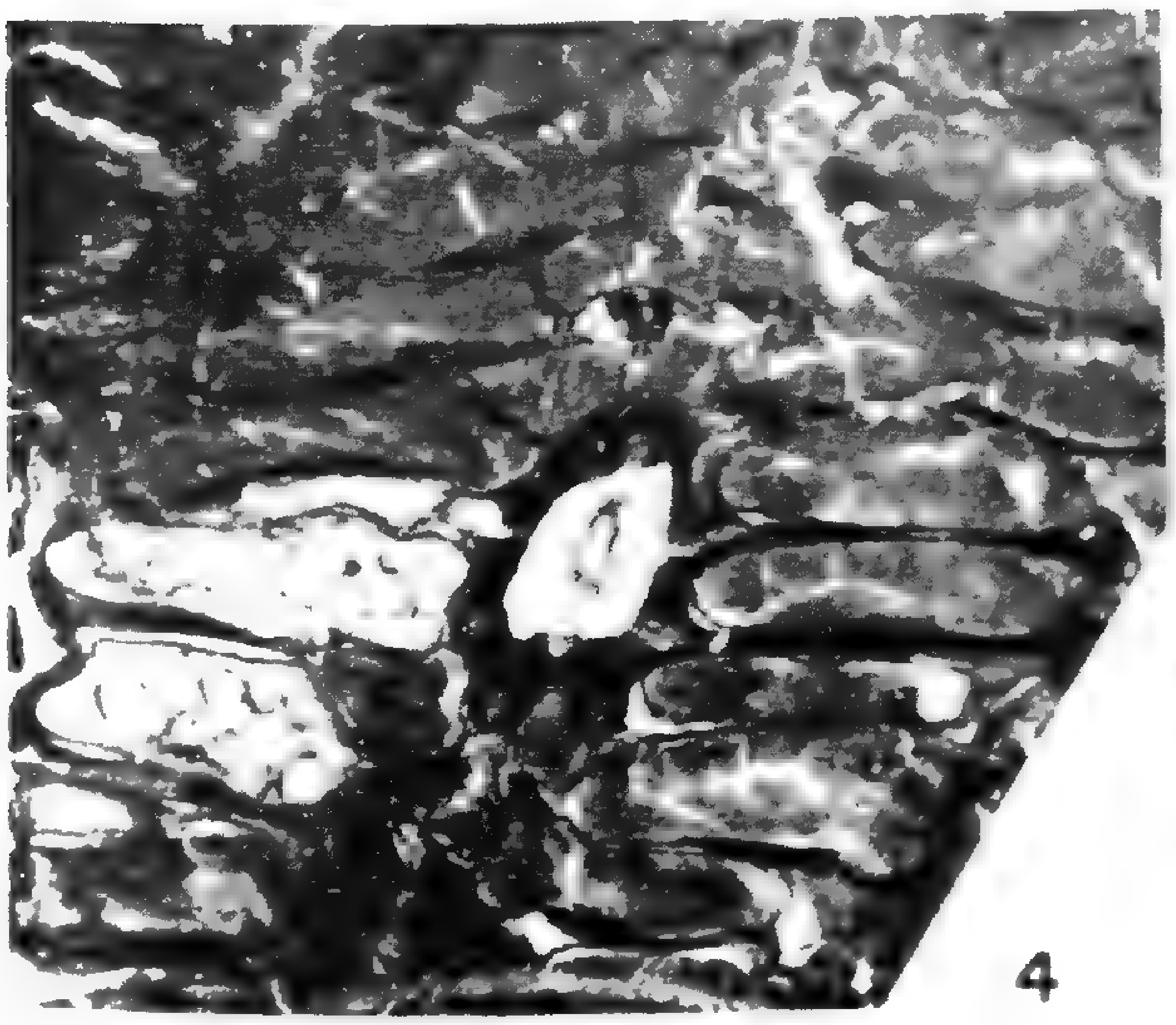
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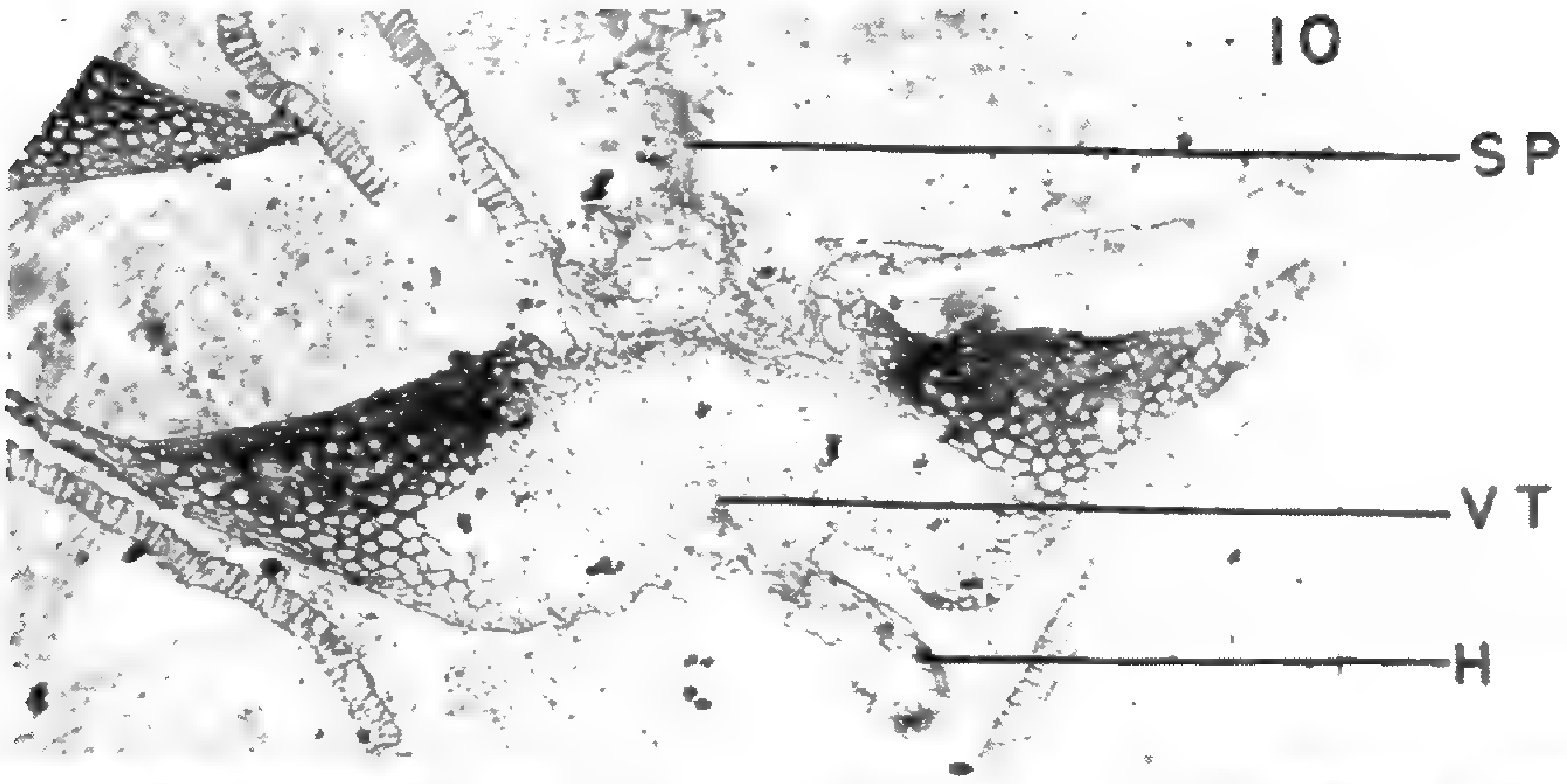
FELIX—ARBORESCENT LYCOPOD FRUCTIFICATIONS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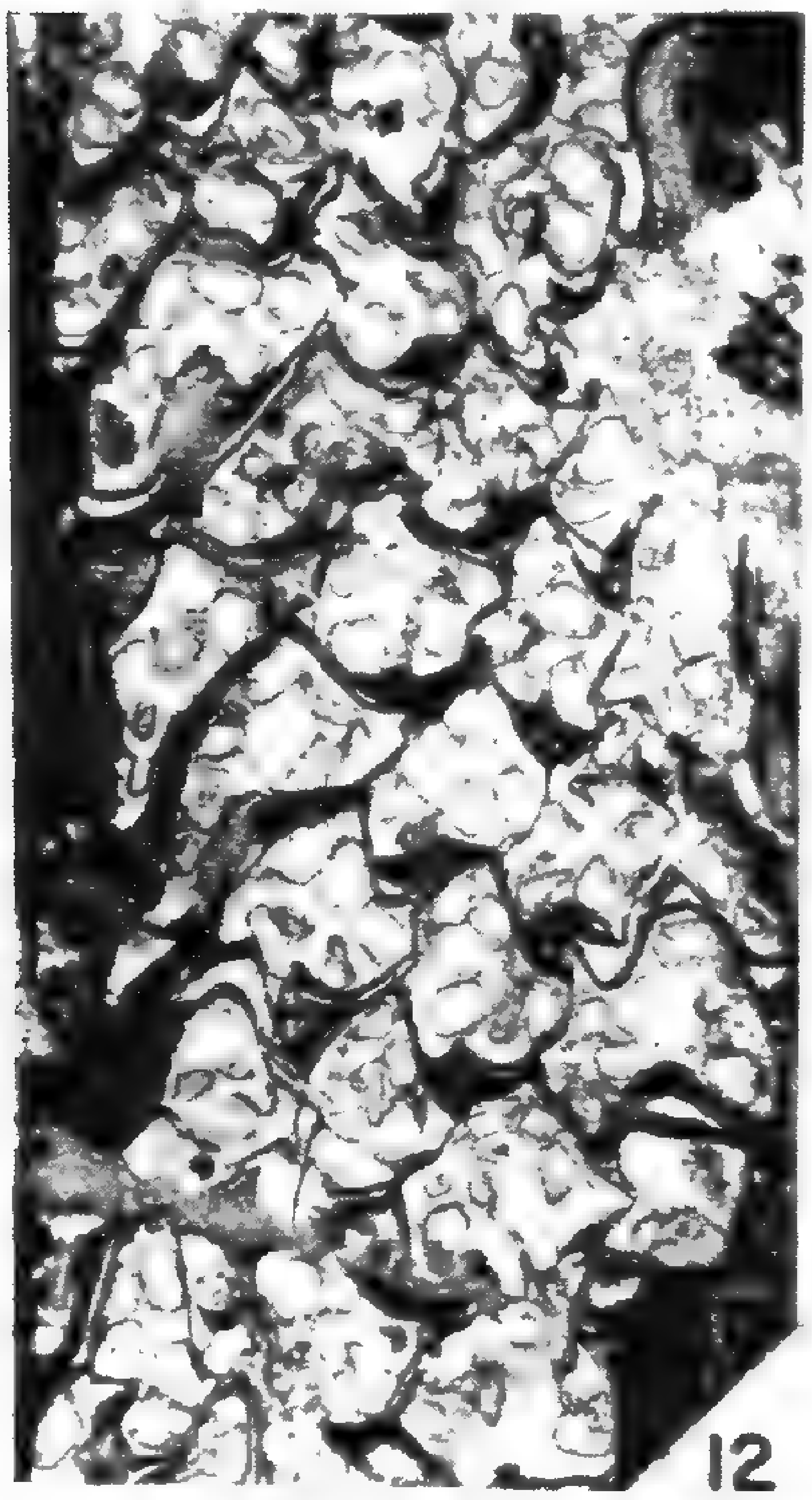
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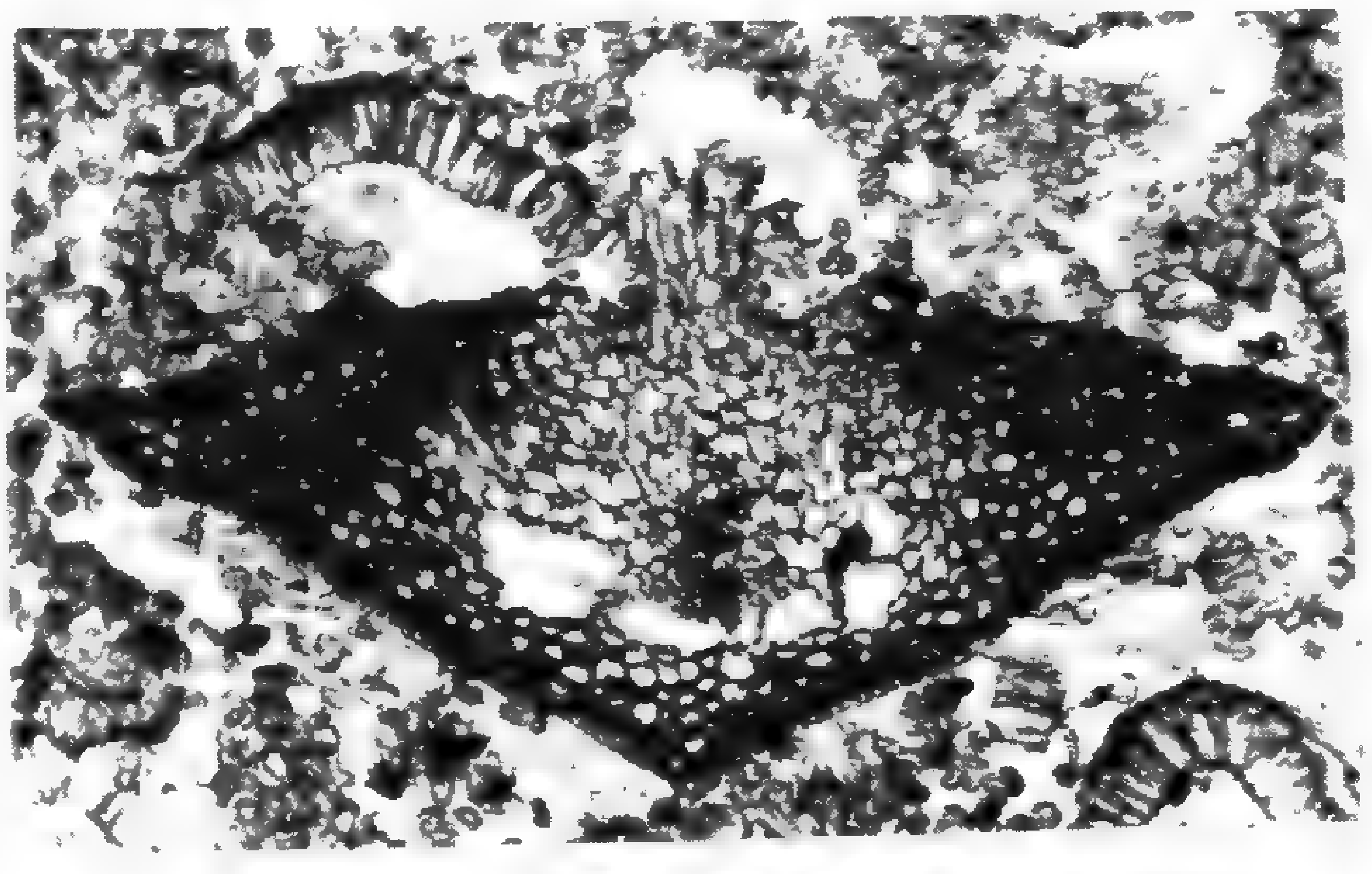
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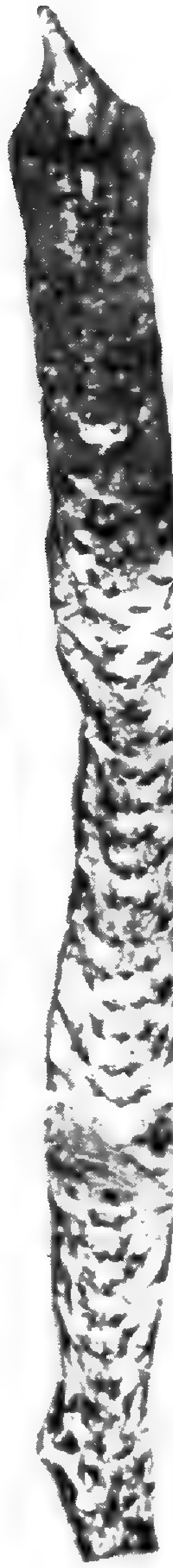
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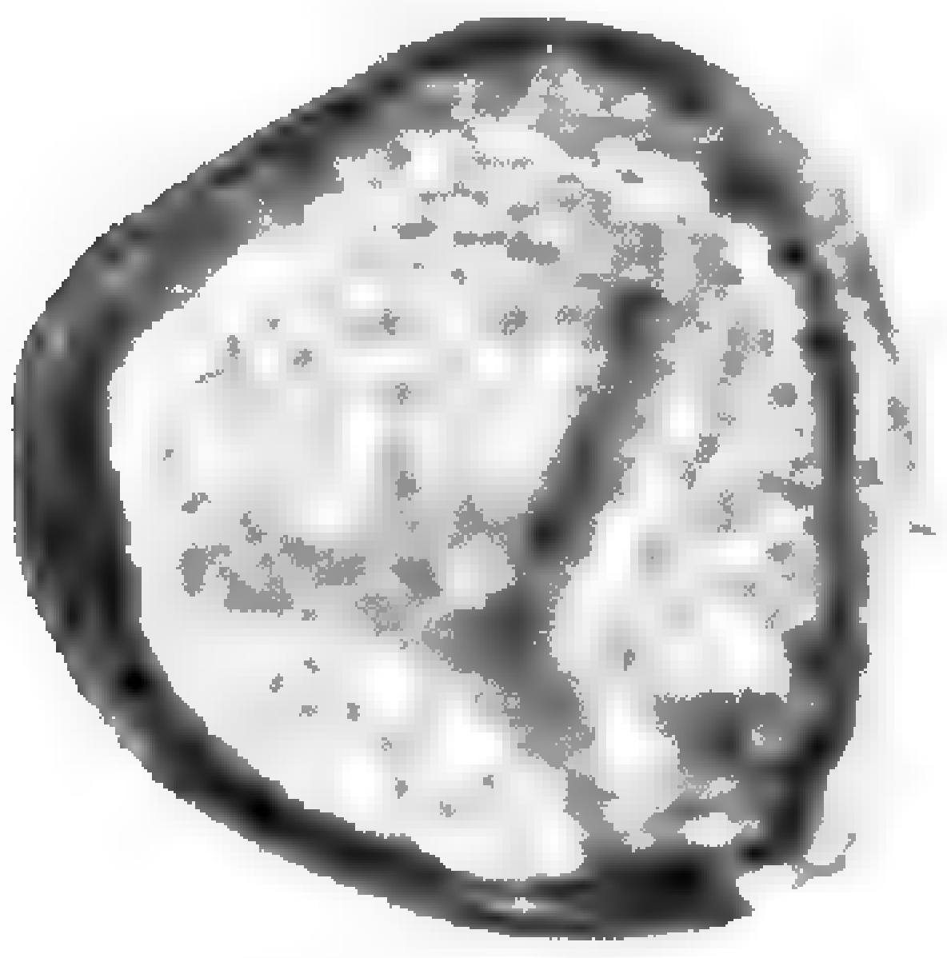
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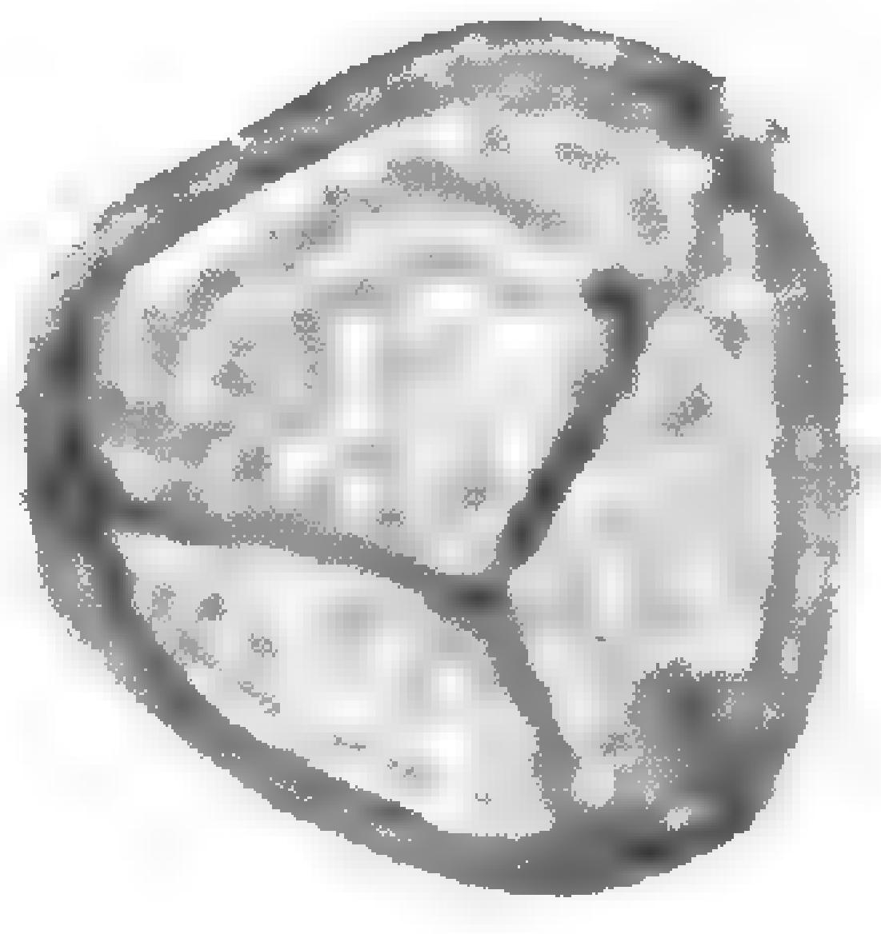
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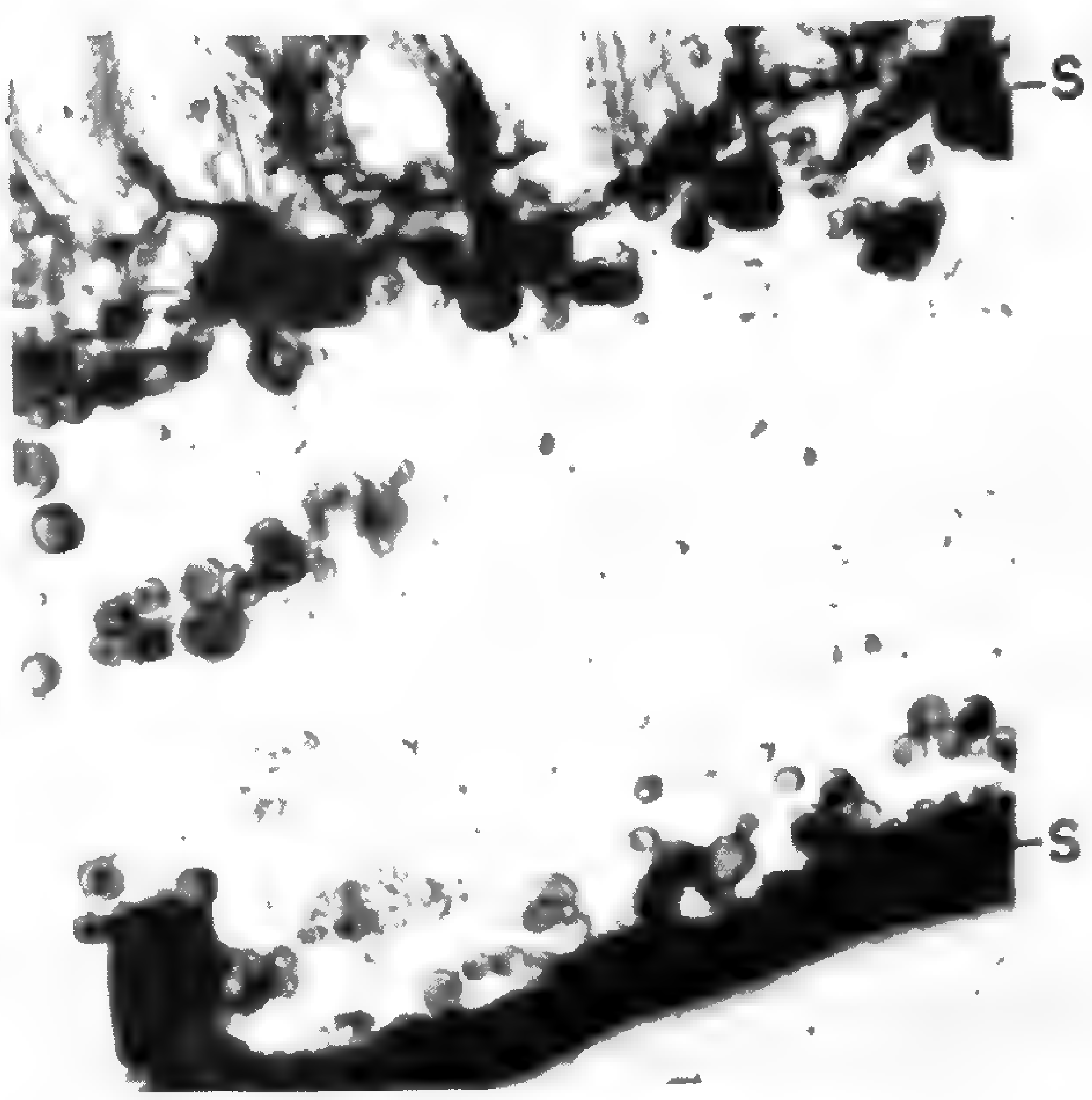
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FELIX—ARBORESCENT LYCOPOD FRUCTIFICATIONS

Explanation of Plate

PLATE 14

Lepidostrobus diversus Felix

Fig. 7. Longisection of cone, showing upper portion containing microspores and lower sporangia dehisced. Serial peels revealed megasporangia in basal portion. WCB 816 A/5, × 1.5.

Fig. 8. Tangential section of sporophyll pedicel near point of departure from cone axis. WCB 816 A/6, × 6.7.

Fig. 9. Tangential section of sporophyll pedicel midway between cone axis and distal end of sporophyll, showing pedicel wings beginning to form. WCB 816 A/6, × 6.7.

Fig. 10. Tangential section near the distal extremity of a sporophyll, showing widely flared pedicel wings: SP, sterile plate tissue; VT, vascular trace; H, heel. WCB 816 B/T8, × 44.

Fig. 11. Radial section of axis, showing course of sporophyll traces. WCB 897, × 35.5.

Fig. 12. Longisection of portion of cone bearing only megasporangia. WCB 818 B/9, × 3.5.

Fig. 13. Section of megasporangium showing cuticular globules: SW, sporangium wall; S, megaspore wall. WCB 851-2, Slide no. 2257, × 415.

Fig. 14. Proximal view of microspore, showing punctations. WCB 857, Slide no. 2247, × 965.

Fig. 15. Proximal view of microspore of fig. 14 in different focal plane, showing equatorial ridge and trilete rays. WCB 857, Slide no. 2247, × 965.

Explanation of Plate

PLATE 15

Lepidostrobus diversus Felix

Fig. 16. Proximal view of microspore, showing width of sutures. WCB 857, Slide no. 2247, × 1150.

Fig. 17. Proximal view of megaspore, showing apical segments and arcuate ridges. WCB 818, Slide no. 2249, × 60.

Fig. 18. Megaspore showing elongate axial dimension. WCB 818, Slide no. 2248, × 60.

Fig. 19. Megaspore showing elongate axial dimension. WCB 818, Slide no. 2248, × 63.5.

Lepidostrobus noei Mathews

Fig. 20. Side view of megaspore, showing spherical shape. Slide no. 2251, × 96.

Fig. 21. View of megaspore of fig. 20, photographed from opposite side. Slide no. 2251, × 96.

Fig. 22. Megaspore of figs. 20 and 21 oriented to show proximal trilete rays. Slide no. 2251, × 96.

Fig. 23. Cuticular globules attached to coat of megaspores of *L. noei*. Slide no. 2250, × 690.

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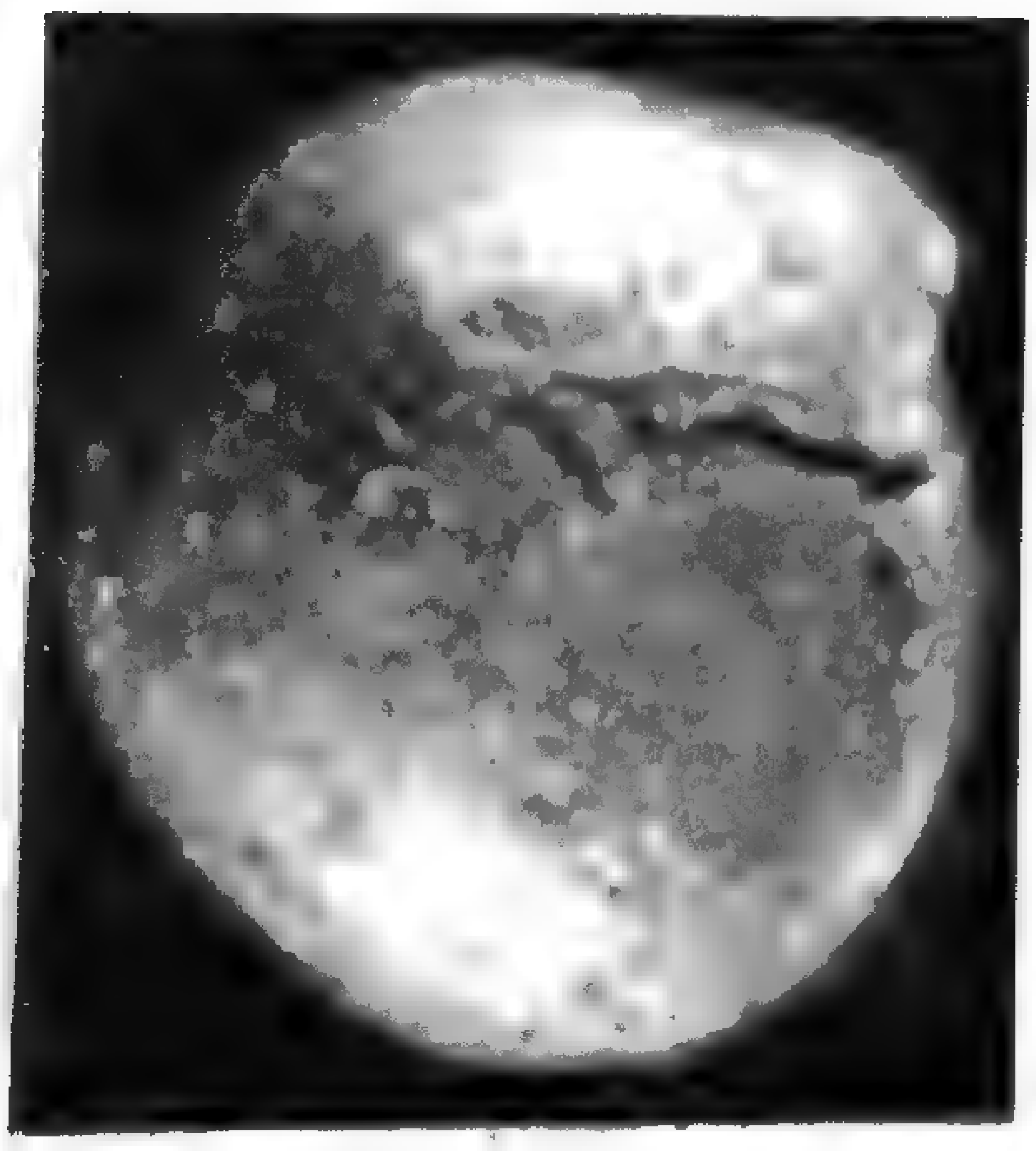

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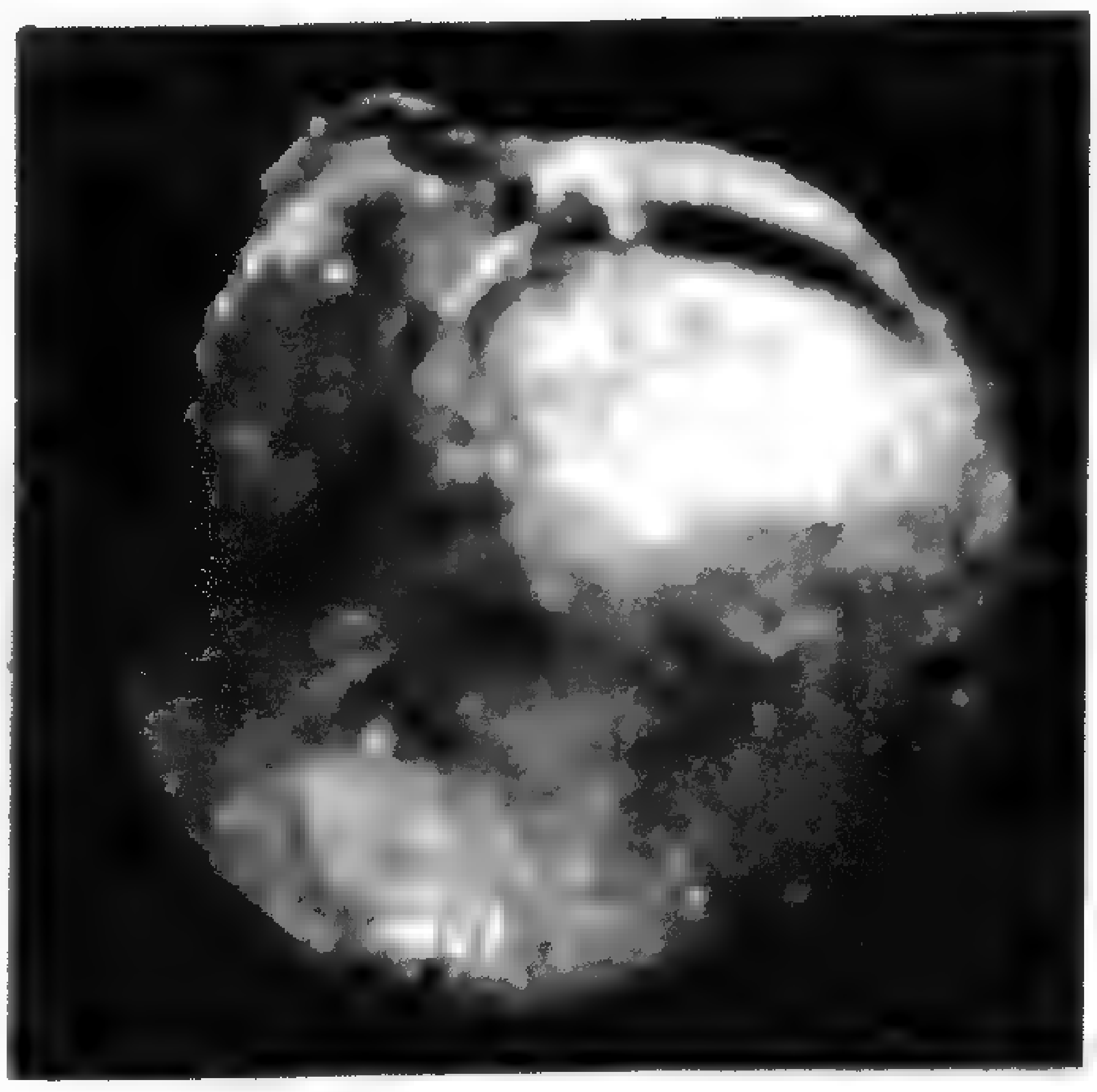

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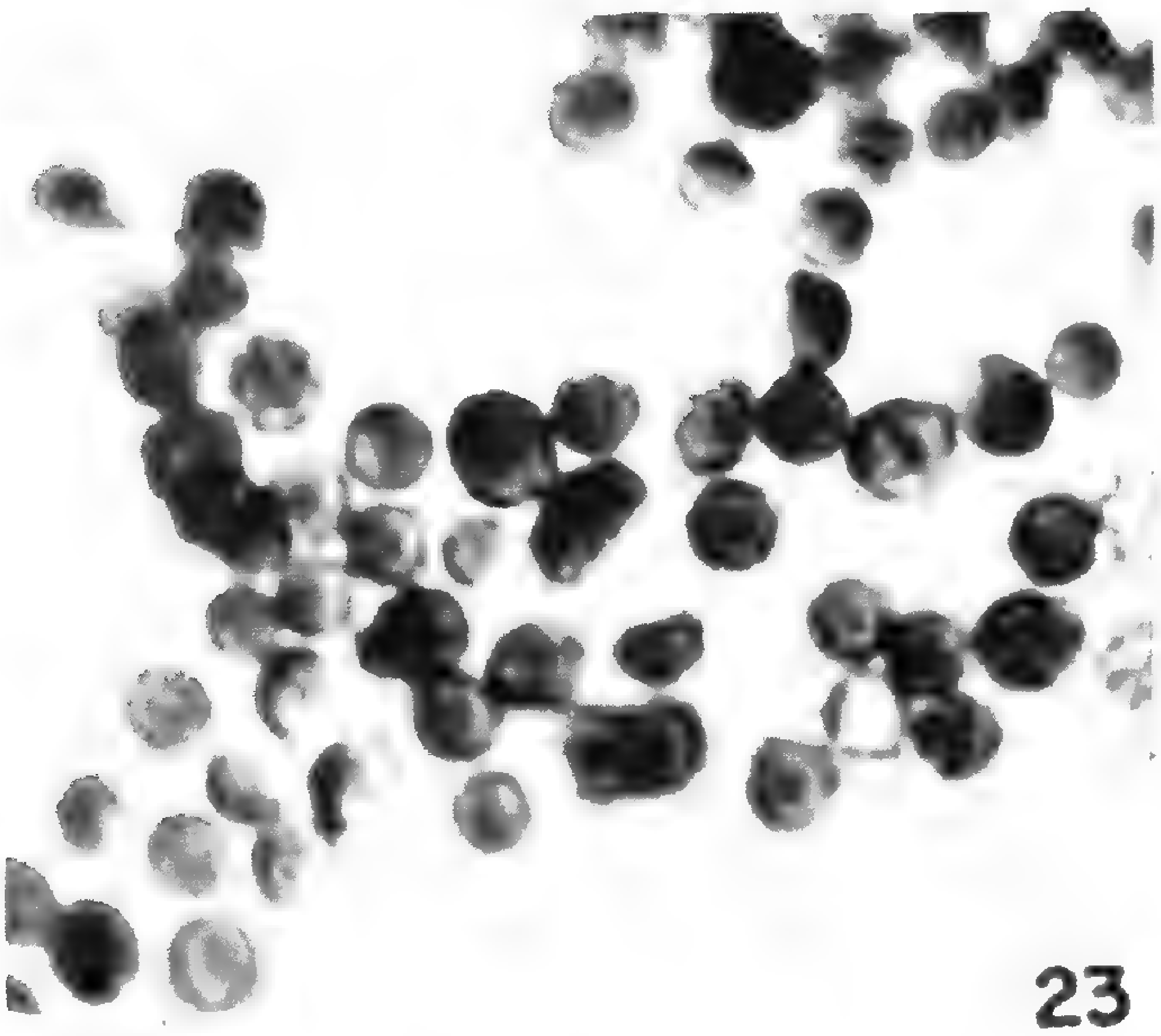

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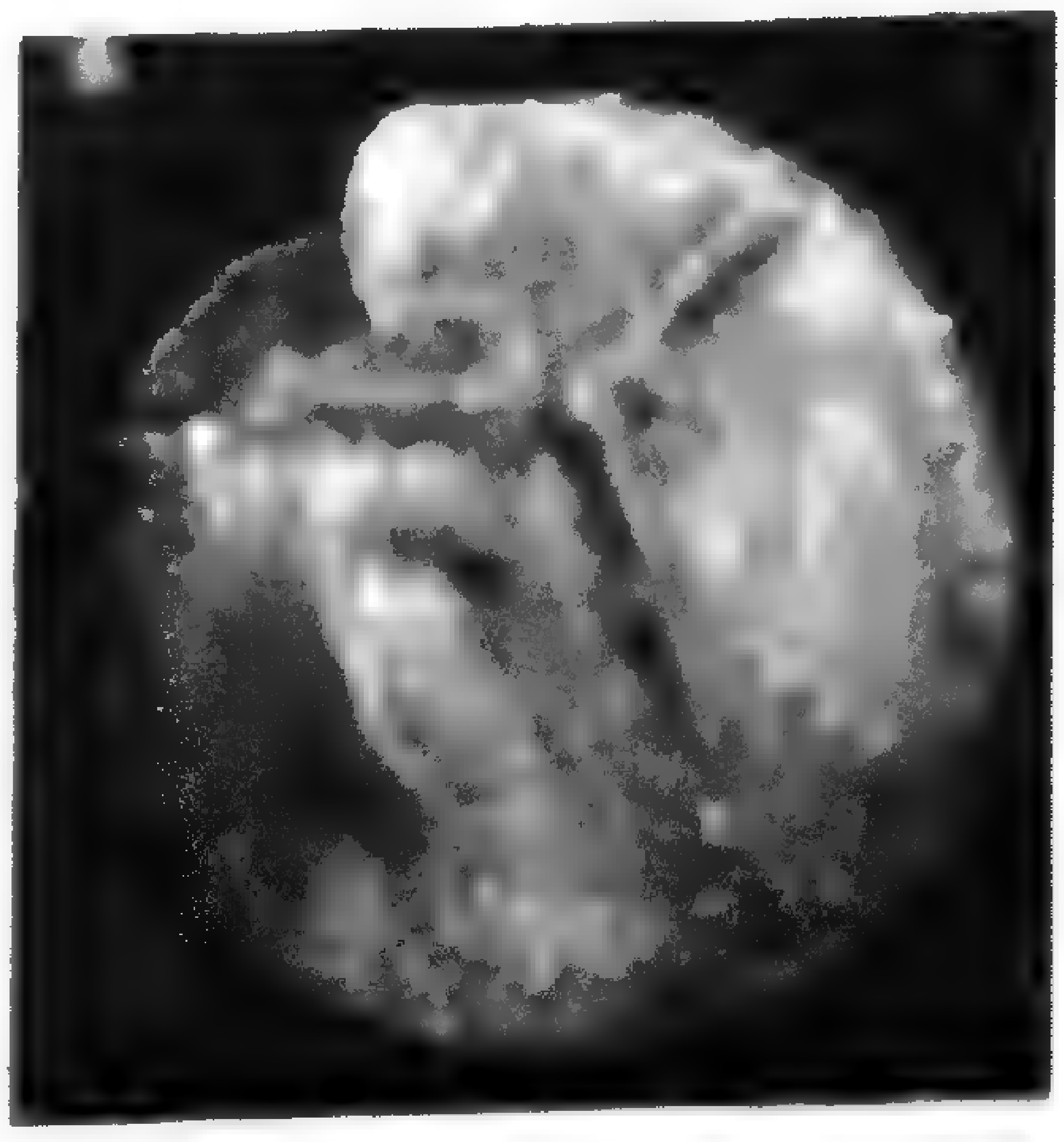

FELIX—ARBORESCENT LYCOPOD FRUCTIFICATIONS

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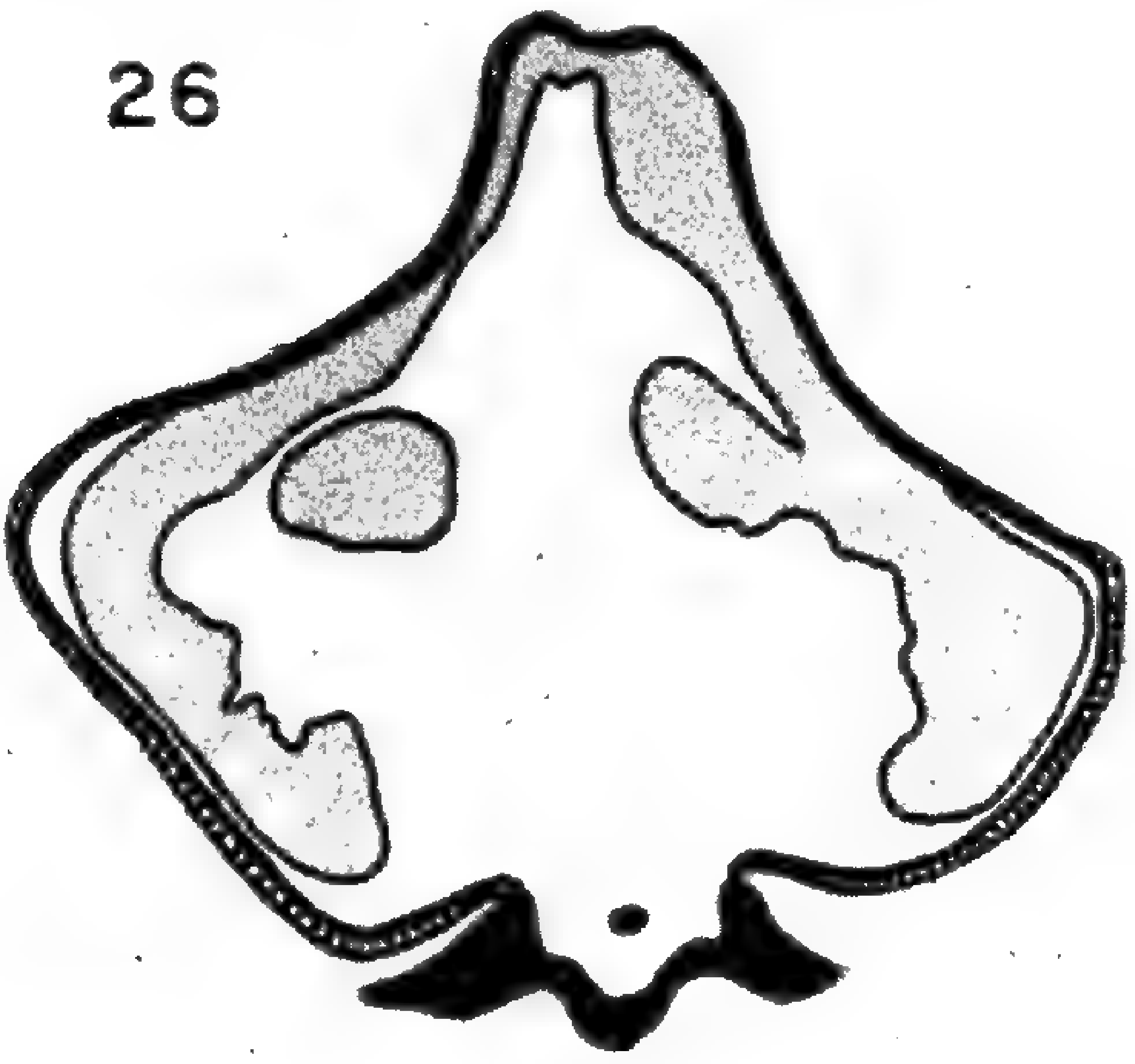

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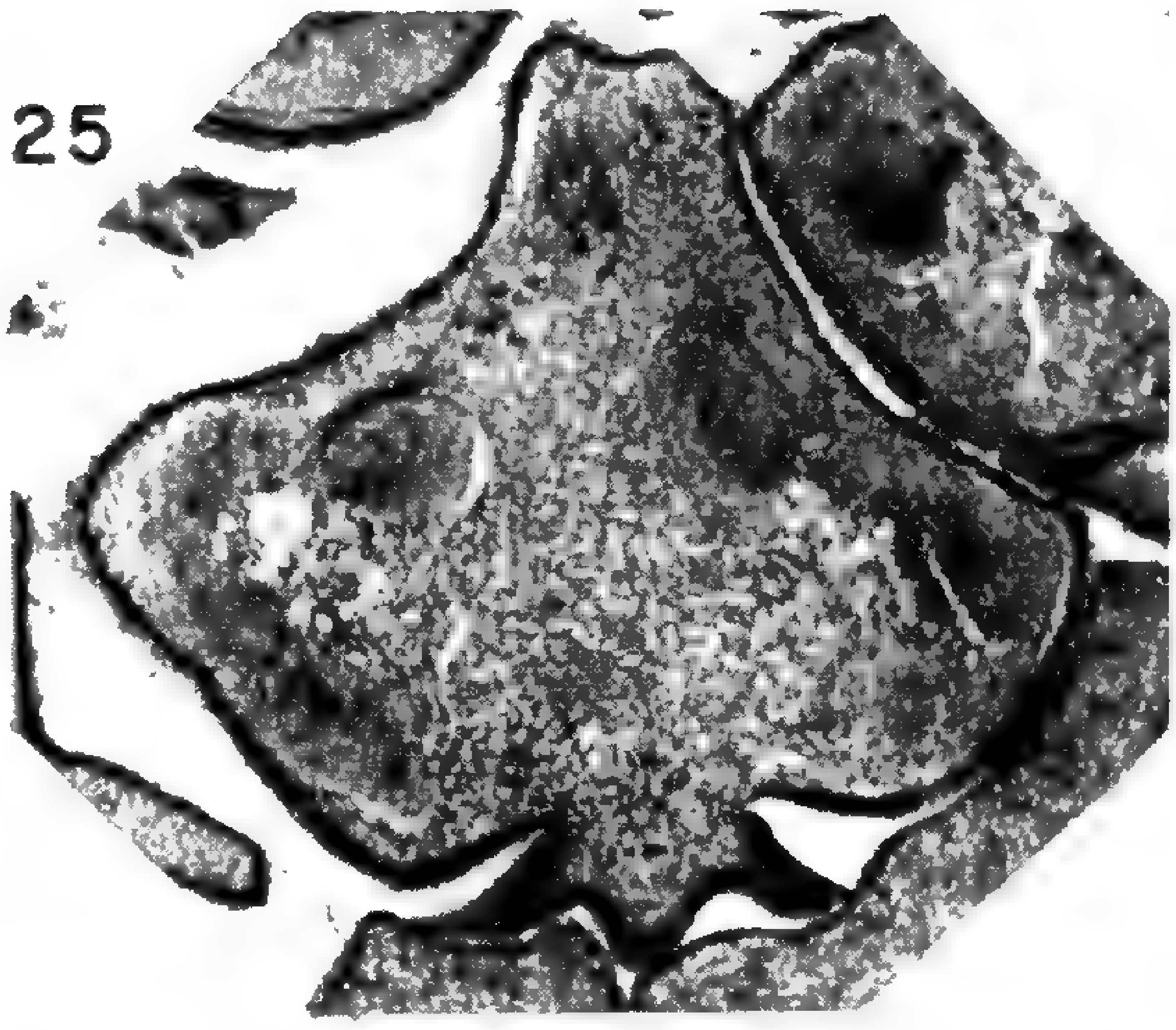

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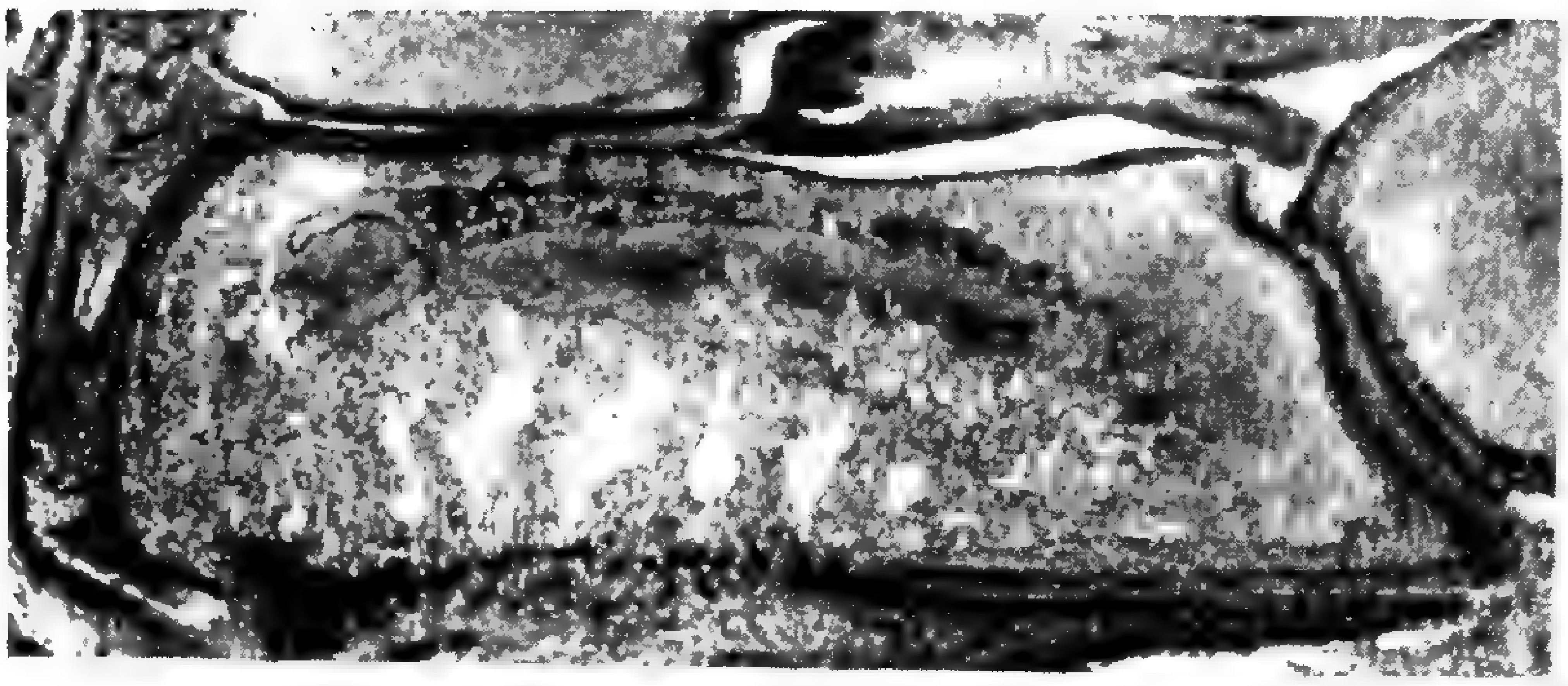

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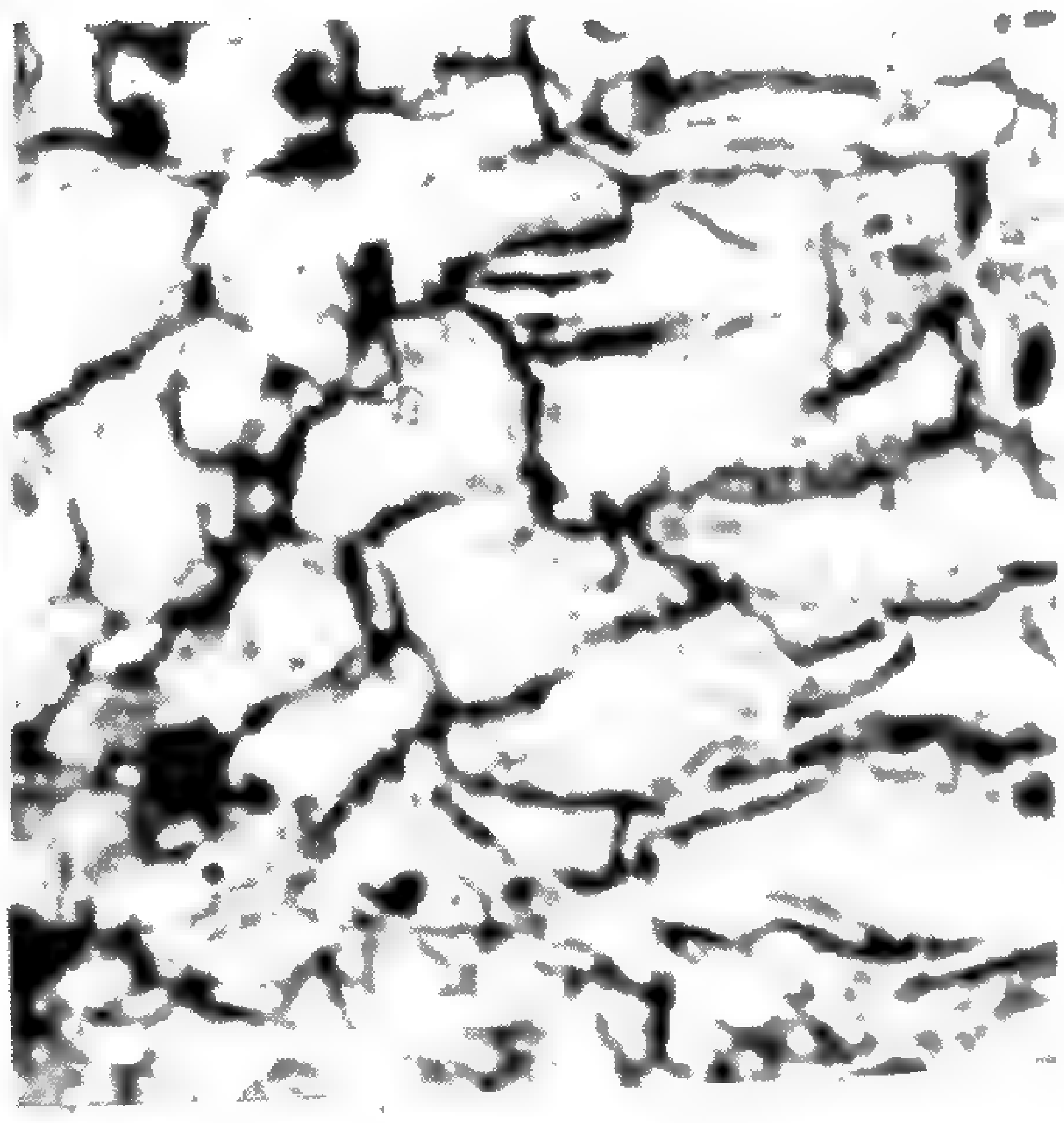

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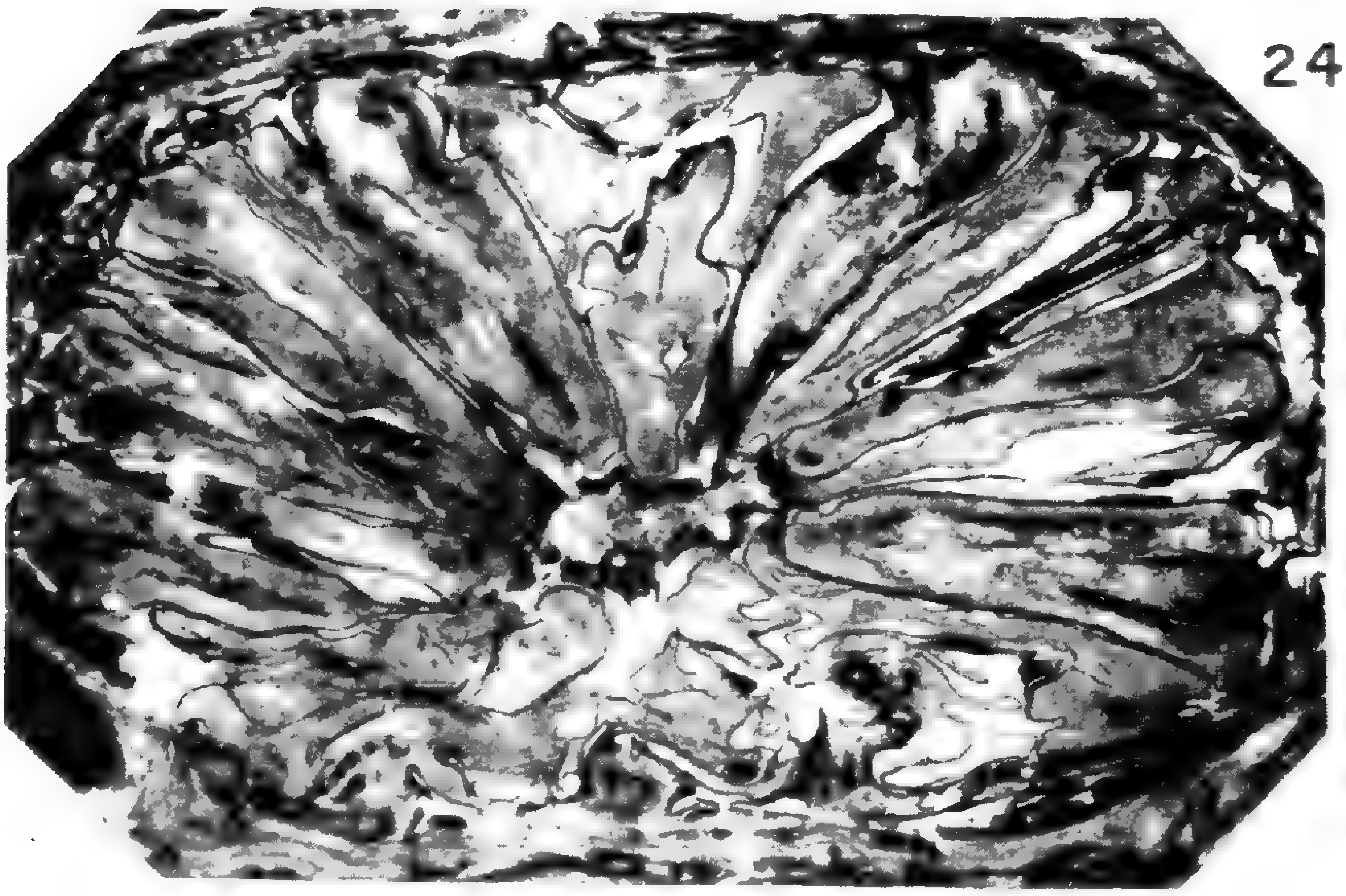

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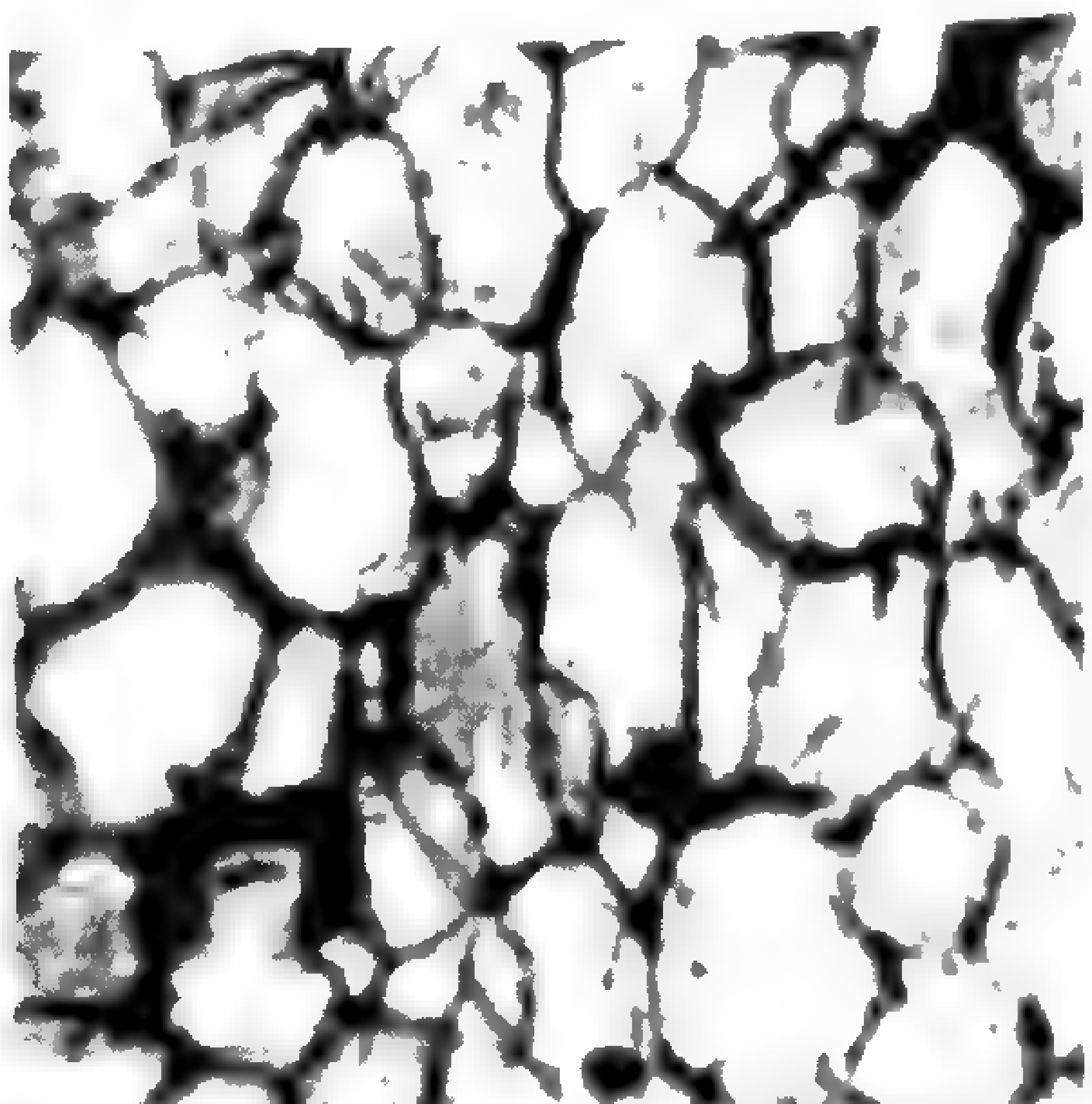

FELIX—ARBORESCENT LYCOPOD FRUCTIFICATIONS

Explanation of Plate

PLATE 16

Lepidostrobus pulvinatus Felix

Fig. 24. Transverse section of cone. WCB 917 B/B10, × 2.2.

Fig. 25. Tangential section of sporangium, showing parenchymatous tissue nearly filling sporangium. WCB 917 C2/S5, × 9.5.

Fig. 26. Diagrammatic sketch of sporangium in fig. 25, showing distribution of spores: stippled portion represents area containing microspores; unstippled portion represents parenchymatous tissue. WCB 917, × 9.5.

Fig. 27. Radial section of sporangium, showing trabeculae. WCB 917 C1/S(2)3, × 6.9.

Fig. 28. Transverse section of sporangium, showing trabeculae. WCB 917 D/T8, × 6.2.

Fig. 29. Basal cells of intrasporangial pad. WCB 917, Slide no. 2268, × 90.

Fig. 30. Cells of intrasporangial pad in upper portion of sporangium. WCB 917, Slide no. 2268, × 90.

Fig. 31. Large microspore which occurred in abundance in basal portion of sporangium. Remnants of a ridge is always evident but preservation is usually poor. WCB 917, Slide no. 2258, × 965.

Explanation of Plate

PLATE 17

Lepidostrobus pulvinatus Felix

Figs. 32–45. Spores removed from a single sporangium of *Lepidostrobus pulvinatus.* WCB 917, all magnifications × 1360.

Fig. 32. Distal view of large spore, showing punctations and equatorial ridge. Slide no. 2263.

Fig. 33. Proximal view of large spore without equatorial ridge. Slide no. 2258.

Fig. 34. Proximal view of large spore with equatorial ridge. Slide no. 2263.

Fig. 35. Proximal view of large spore with equatorial ridge. This type composed a high percentage. Slide no. 2263.

Figs. 36–38. Proximal views of medium-sized spores, showing variations in equatorial ridge. Fig. 36, Slide no. 2259; fig. 37, Slide no. 2263; fig. 38, Slide no. 2258.

Fig. 39. Proximal view of spore found near top of central pad of tissue, showing brown cuticular bodies on spore coat. Slide no. 2258.

Figs. 40–42. Proximal views of smaller spores found in upper part of the sporangium. Figs. 40, 42, Slide no. 2259; fig. 41, Slide no. 2258.

Fig. 43. Spore tetrad occurring in large numbers in upper part of sporangium. Slide no. 2259.

Fig. 44. Portion of tetrad. Slide no. 2258.

Fig. 45. Large flattened spore, showing punctations. Slide no. 2259.

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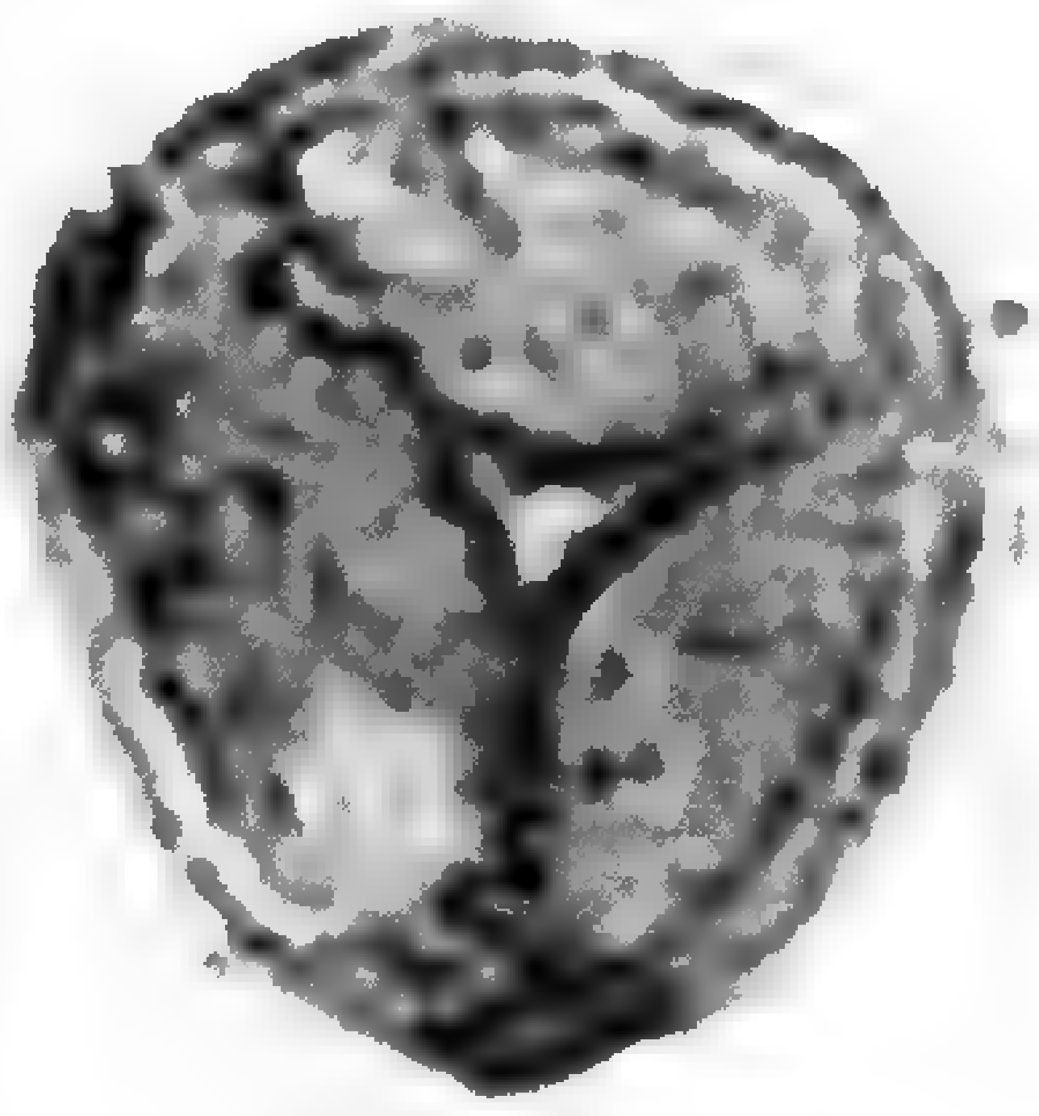

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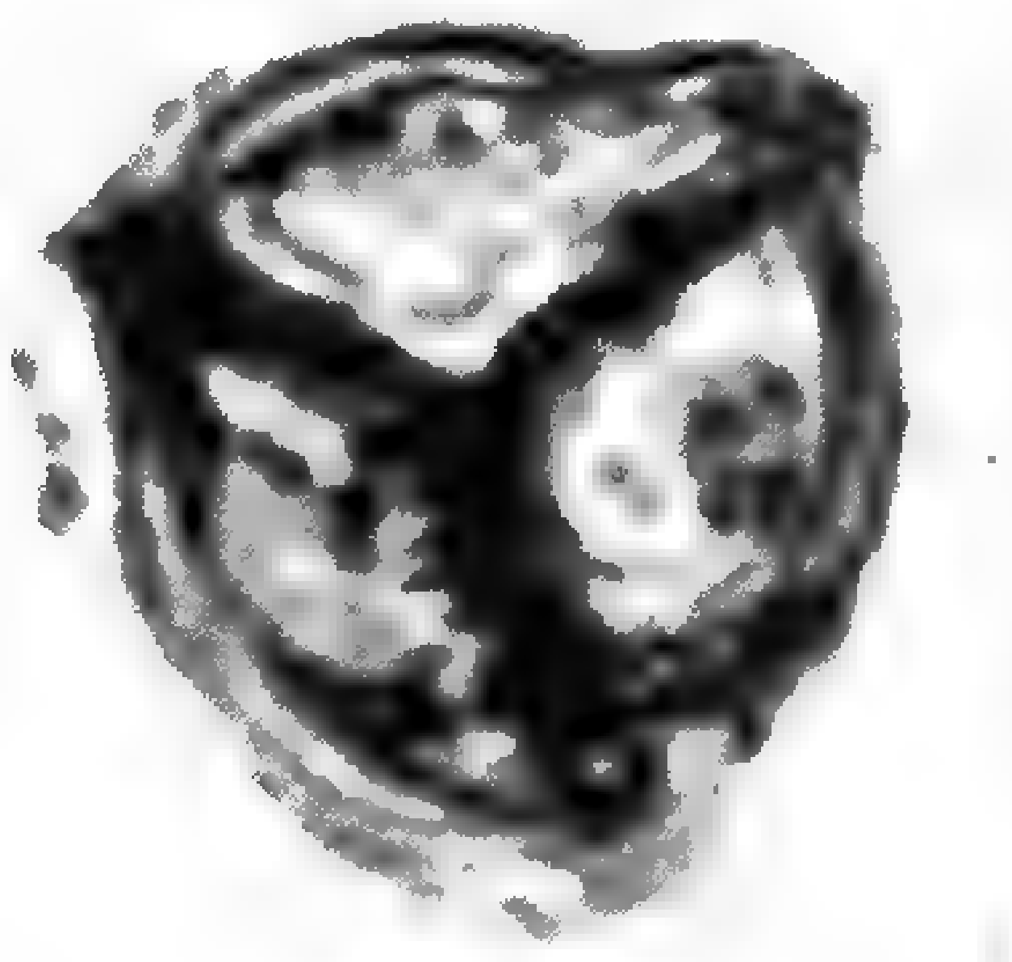

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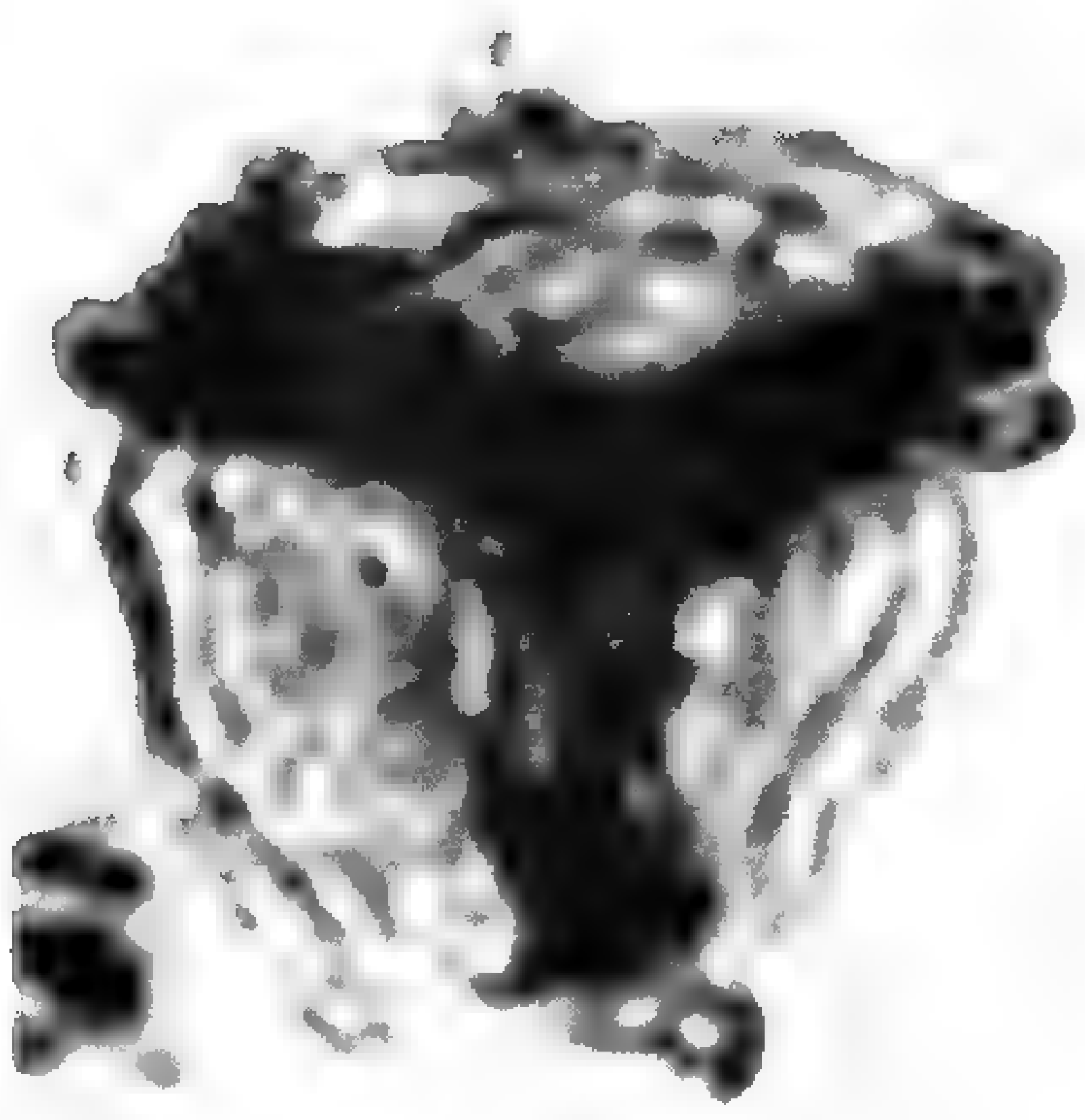

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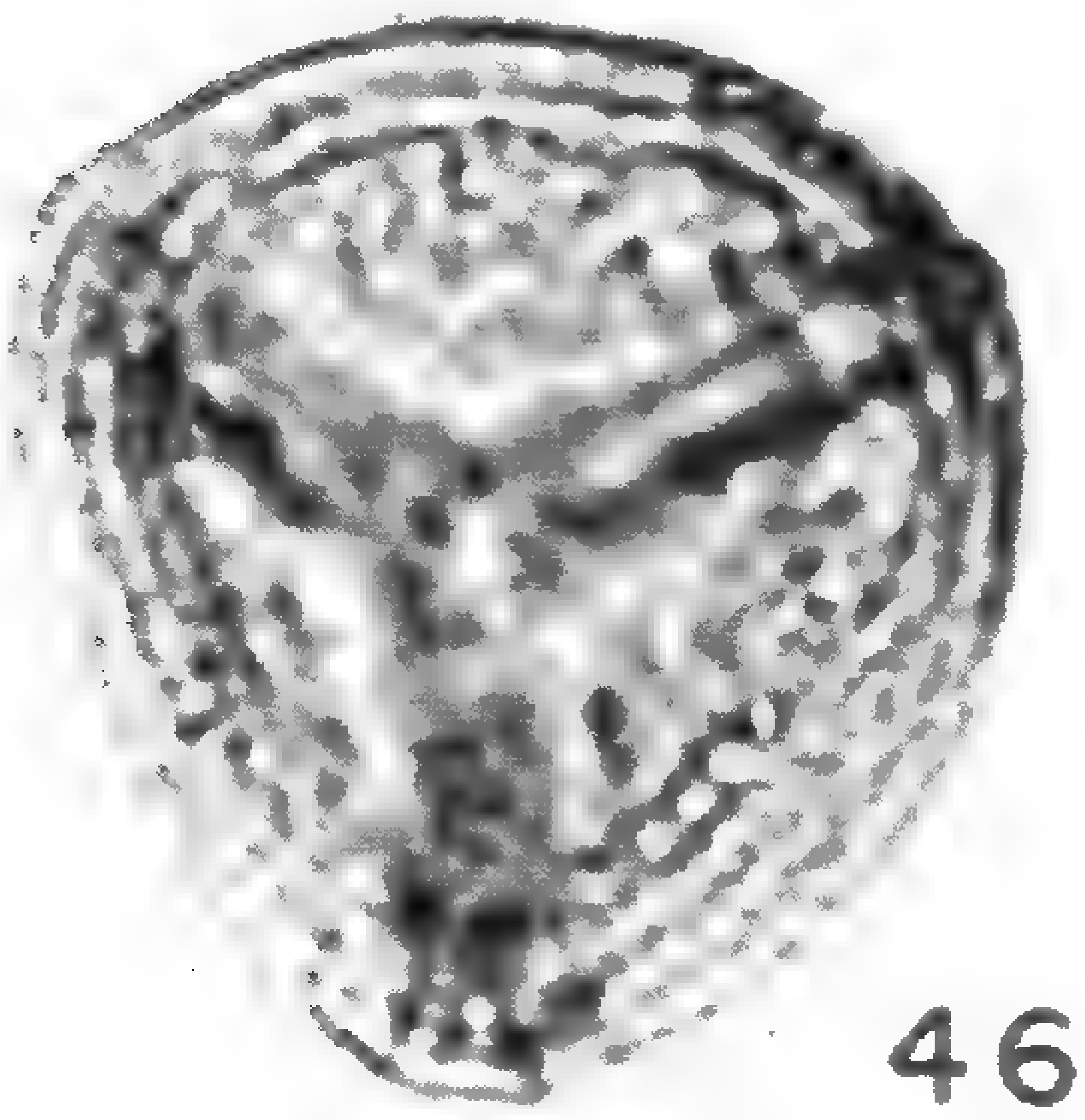
FELIX—ARBORESCENT LYCOPOD FRUCTIFICATIONS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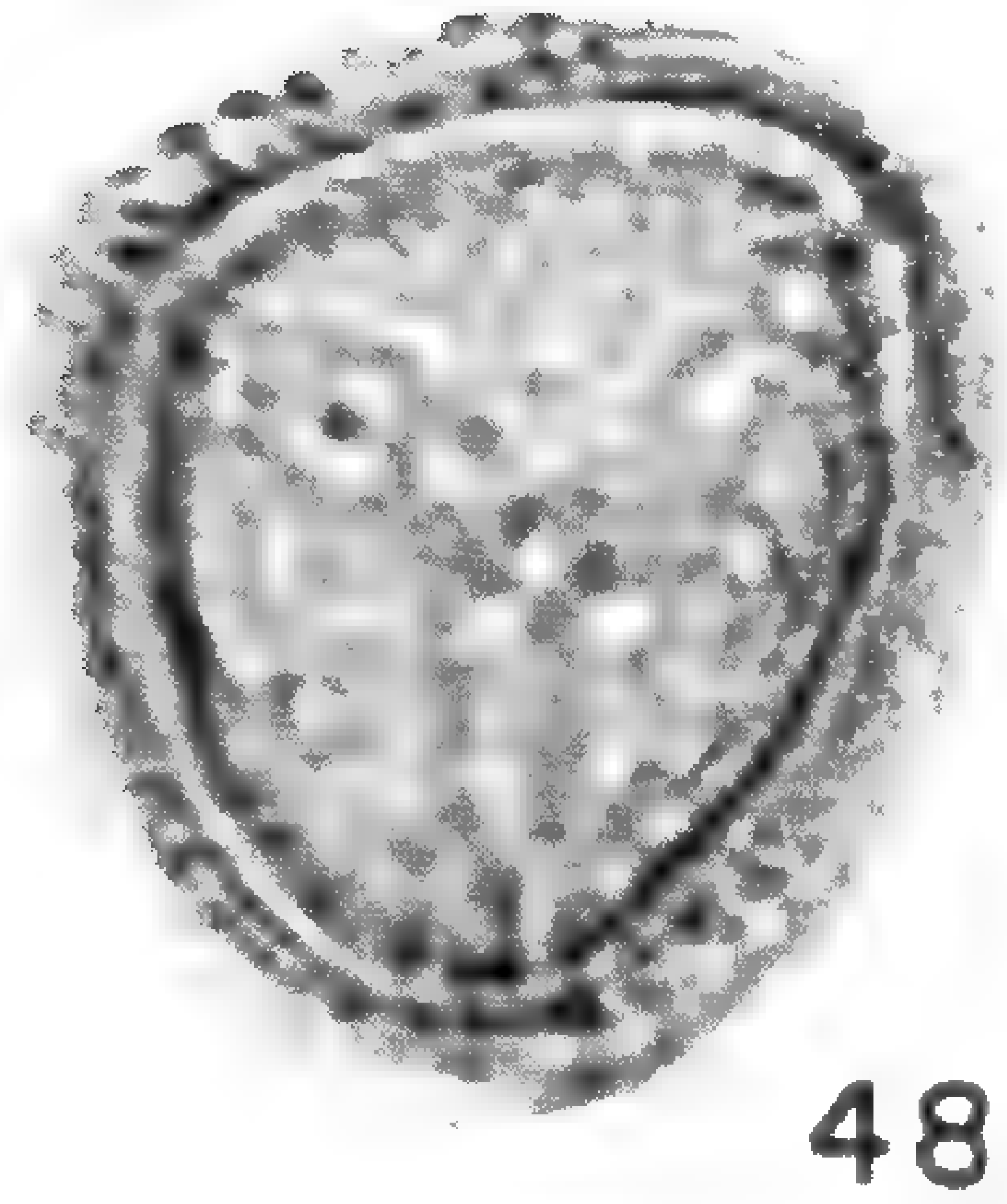
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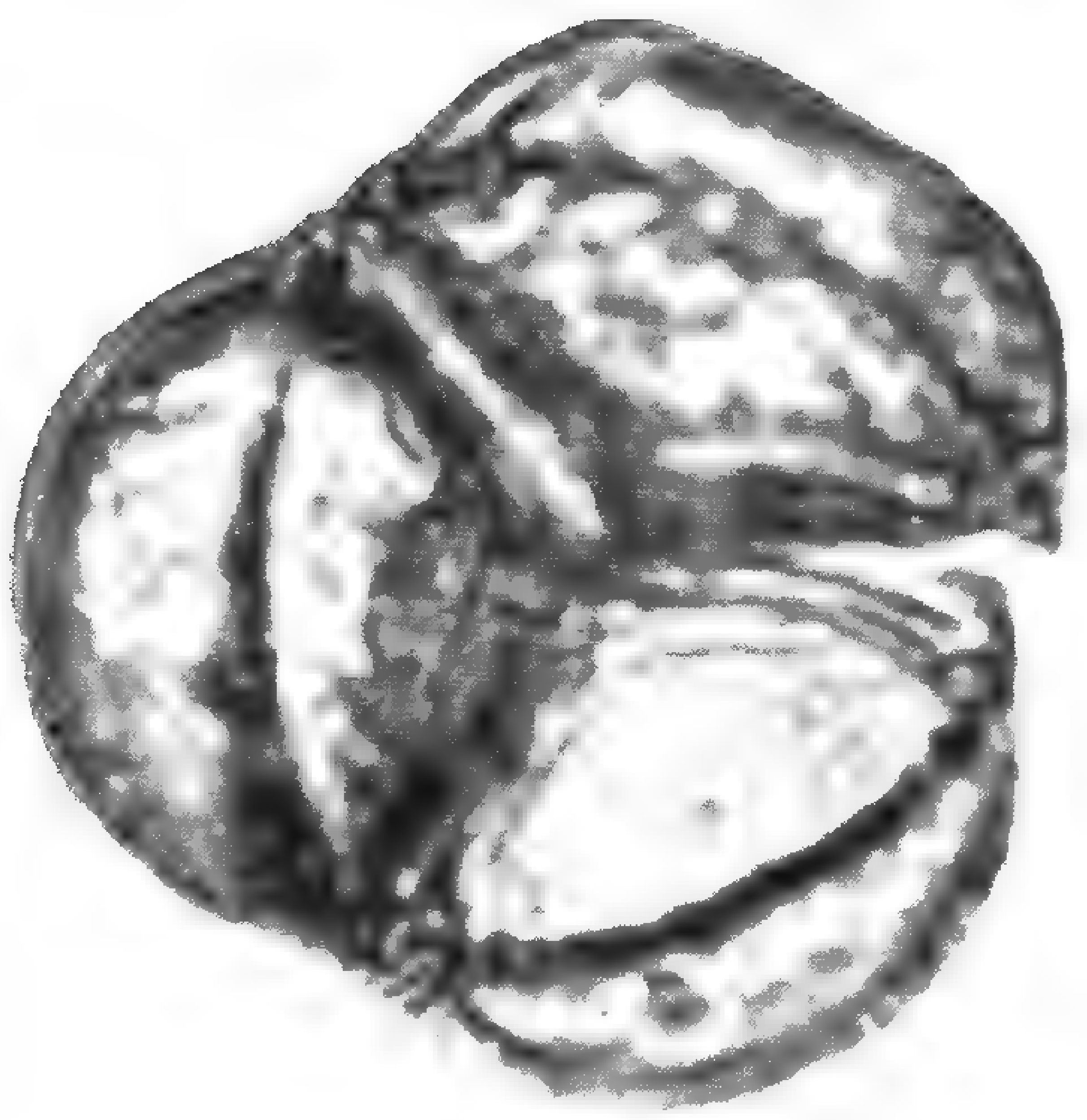
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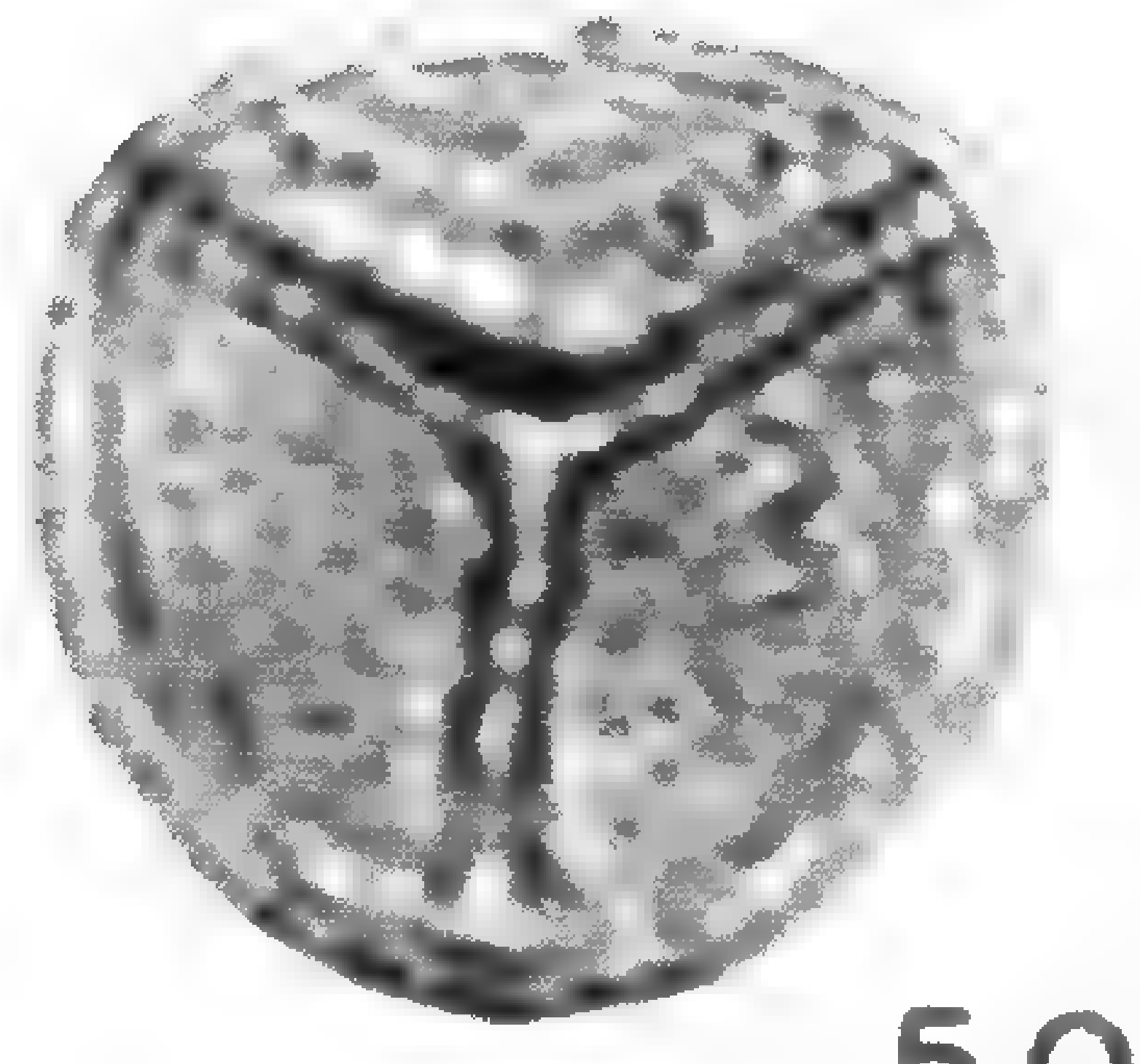
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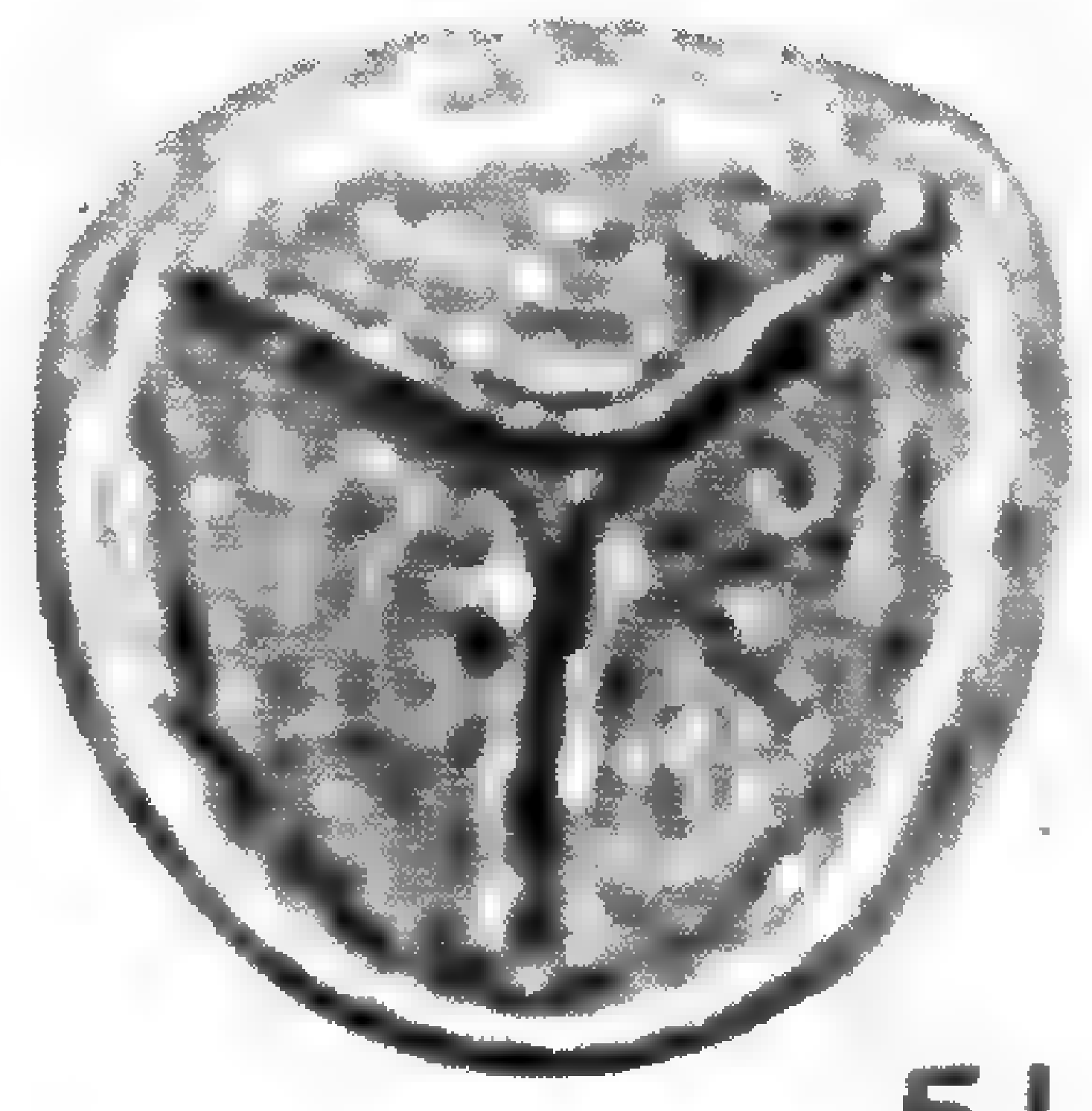
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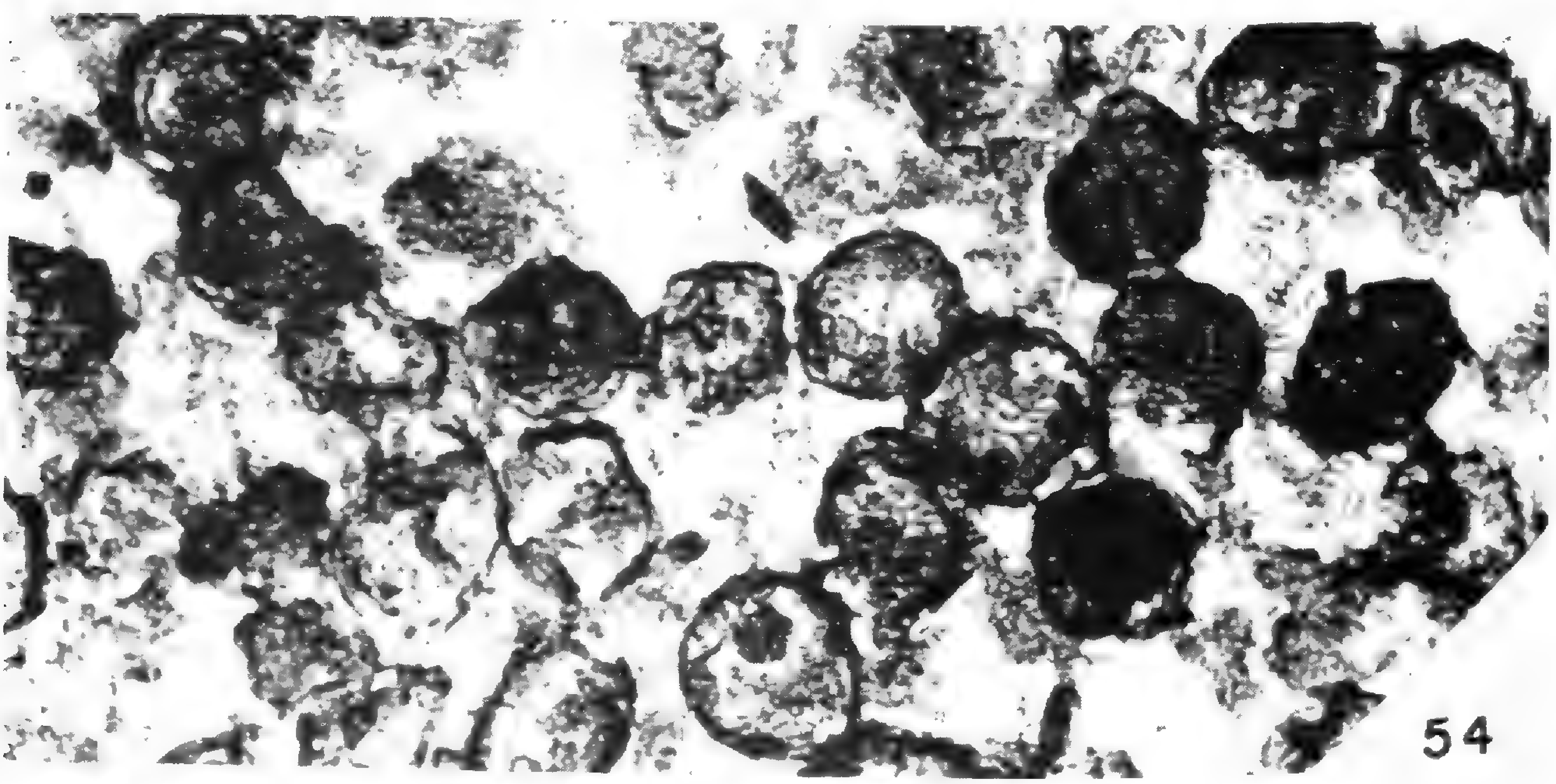
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FELIX—ARBORESCENT LYCOPOD FRUCTIFICATIONS

Explanation of Plate

PLATE 18

Lepidocarpon magnificum Andrews & Pannell

Figs. 46–47. Proximal view of spores, showing ornamentation and ridge characteristics. WCB 166, Slide no. 2316, × 1295.

Fig. 48. Distal view of spore. WCB 166, Slide no. 2316, × 1295.

Lepidocarpon sp. (except fig. 54)

Fig. 49. Spore tetrad, showing equatorial ridges. WCB 847B, Slide no. 2317, × 1295.

Fig. 50. Proximal view of spore, showing punctations and trilete sutures. WCB 847B, Slide no. 2317, × 1295.

Fig. 51. Spore of fig. 50 in different plane of focus, showing equatorial ridge. WCB 847B, Slide no. 2317, × 1295.

Fig. 52. Proximal view of spore. WCB 847B, Slide no. 2317, × 1295.

Fig. 53. Distal view of spore. WCB 847B, Slide no. 2317, × 1295.

Fig. 54. Fungal-like spores present within lepidocarp seed shown in fig. 59. Slide no. 2255, × 260.

Explanation of Plate

PLATE 19

Lepidocarpon crenatum Felix (except figs. 58, 59)

Fig. 55. Photograph of detached specimen. WCB 816B, × 7.6.

Fig. 56. Epidermal protuberances near base of specimen. WCB 816B, Slide no. 2252, × 82.

Fig. 57. Epidermal protuberances of integument near the micropylar opening. WCB 816B, Slide no. 2252, × 82.

Fig. 58. Integumented lepidocarp, containing probable fungal spores. Slide no. 2254, × 8.2.

Fig. 59. Integumented lepidocarp, containing probable fungal spores. Slide no. 2255, × 7.6.

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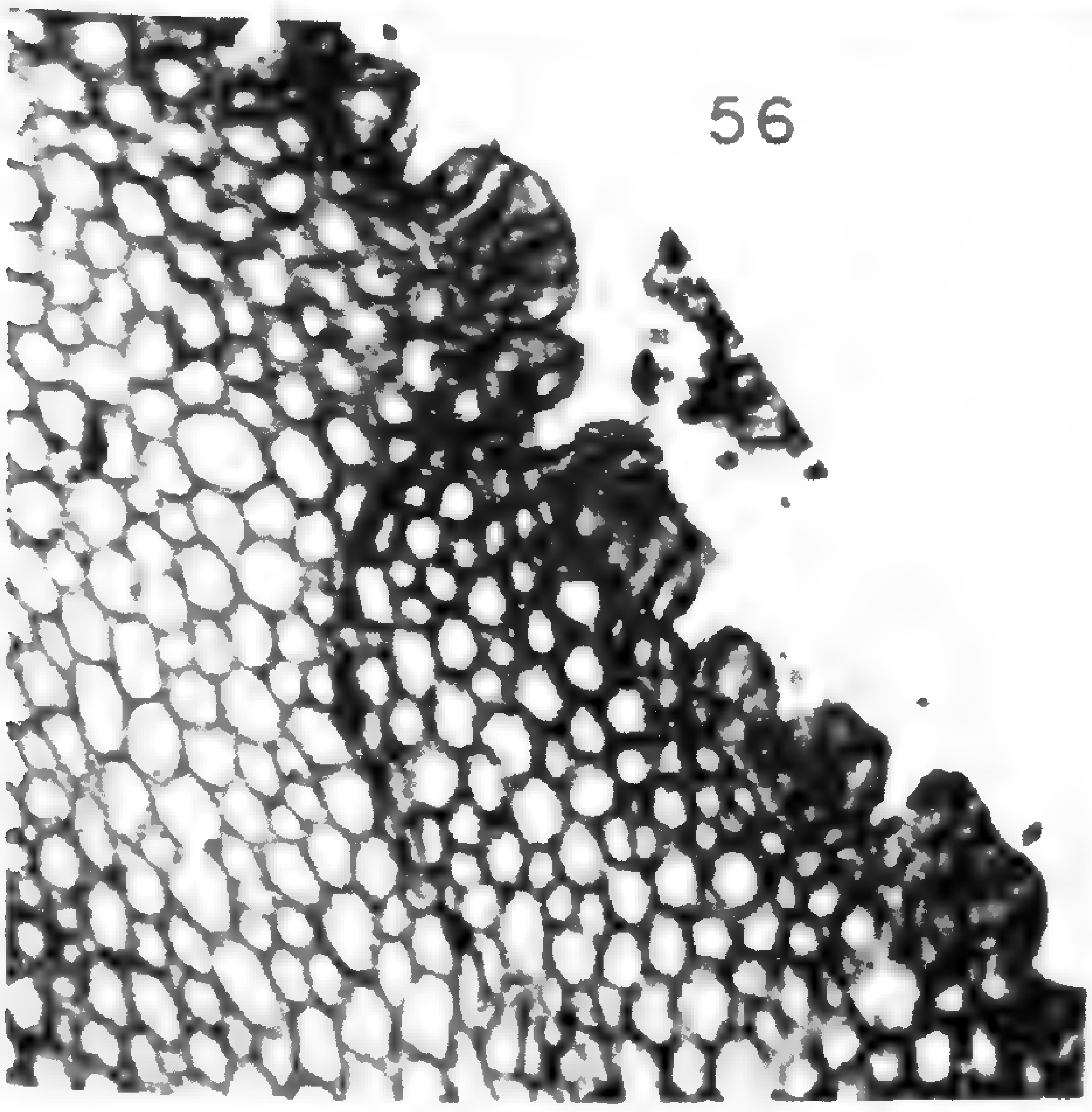

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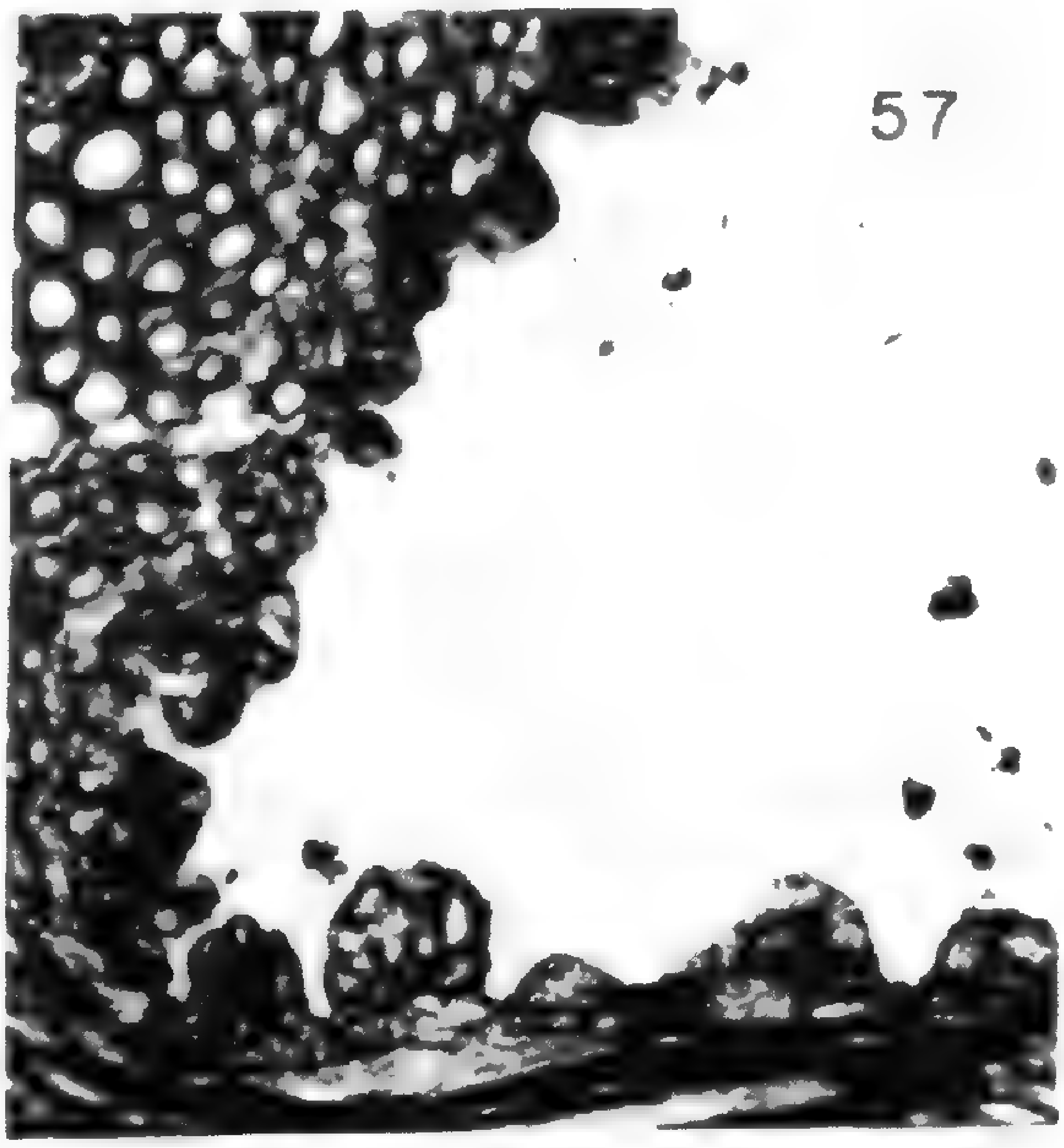

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FELIX—ARBORESCENT LYCOPOD FRUCTIFICATIONS

A Study of American Petrified Calamites

BURTON R. ANDERSON

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A STUDY OF AMERICAN PETRIFIED CALAMITES[1]

BURTON R. ANDERSON

The only extensive account of American petrified calamites is that by Andrews (1952), based on a portion of the collection of calamites in his laboratory. Since that time a large number of specimens has been added to this collection which forms the basis for the present investigation. From a study of these it has been possible to determine significant criteria for evaluating species of stem fragments, to record European species as present in American coal balls, and to give definite statistics for established American species. A number of stems fall into two new species, and one fragment is apparently new but too poorly preserved to receive specific assignment. Roots are numerous, and two new species are described. A few coal balls contain an abundance of leaves of a new species sometimes found in connection with twigs. Of special interest is a new species of cone, the first calamitean cone to be described from American coal balls. Finally, a stratigraphic and geographic tabulation is presented based on material within the scope of this investigation.

STEMS

Most of the work on petrified stems has been done by Williamson, Renault and Knoell. Williamson (1871, 1871a, 1878, 1883; Williamson and Scott, 1895, 1895a) described calamites and other fossil plant groups almost strictly from a morphological and anatomical viewpoint. He was loath to found species upon fragments of plants but was not unaware that some variation in stems was specific, and in one instance he did itemize variations of primary rays. Most of the taxonomic work was done by Renault (1885, 1886, 1895–1898) who used a variety of characters to distinguish species. Some characters are sound, such as pitting in tracheids, variation in primary and secondary rays, and orientation of primary tissues; but others, such as internode length based on one small fragment, regularity and frequency of branching, and pith and stem diameter, have proved to be unreliable. Also, varieties of *Arthropitys bistriata* (Cotta) Goeppert were formed on differences that would appear to be clearly specific. Knoell (1935) described some new species and varieties of stems but did not correlate them with previously described species. The use of characters observed chiefly from cross-sectional views is an additional confusing aspect of her work. *Arthropitys communis* was split into two entities, the species and a variety, based upon difference in the manner of primary ray diminution. The species was more closely defined and therefore designated as a new combination, *Arthropitys communis* (Binney) Hirmer & Knoell. This new combination is not valid and the correct name should be *Arthropitys communis* (Binney) Renault.

---

[1] An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

It is apparent from the literature that taxonomy of calamitean stems is inconsistent, and unreliable criteria have sometimes been used to separate species. For purposes of clarification the following is a suggested evaluation of stem characters offered as a guide to the delimitation of species.

I. *Stem Diameter.*—As a distinguishing character this is probably totally unreliable. Only *Arthropitys gigas* (Brongniart) Renault is partially distinct because of its large size.

II. *Internode Length.*—From a study of impression calamites the wide range of internode lengths in one specimen is immediately apparent. In petrified stems it is best to avoid using this feature unless it is constant in several specimens.

III. *Branching.*—This is a major feature in classifying impression calamites. However, unless a petrifaction is so well preserved that its branching can be correlated with impression types, it has little diagnostic value.

IV. *Pith.*—Whether or not pith is preserved at the periphery and as nodal discs is a matter of age of the stem or fossilization conditions. Pith is the same in all calamitean stems: large, unordered, thin-walled parenchyma. Sometimes dark-colored cells are seen singly or in groups and are of diagnostic value and called resinous cells by some paleobotanists.

V. *Primary Wood.*—Primary wood of each pole is of small amount and borders the protoxylem canal on the outer side. Written description does not serve well to characterize primary wood. Orientation of pith cells about the pole, orientation of tracheids about the protoxylem canal, and relationships with secondary wood—all form a picture varying in each species, and unless illustrated they are of little diagnostic value. Caution is necessary in using the size of the protoxylem canal, for it varies with pith diameter somewhat. This also holds true for the distance between protoxylem poles and width of the fascicular segment. The problem of whether primary wood of the Calamitaceae had endarch or mesarch development has never been resolved, although most authors believe in endarch development for the family. Andrews (1952) described a specimen from Mineral, Kansas, that has a relatively large amount of small, thick-walled cells surrounding the protoxylem canal, giving the appearance of mesarch development. Appropriate radial sections showed no pitting on the cells centripetal to the canal, but this is no disproof of centripetal xylem since preservation is far from good. Despite subsequent collection of a large number of stems from the Kansas locality, none of them are of his "species A" type.

VI. *Fascicular Segment.*—This structure, as a whole, is somewhat stereotyped although its width near the primary wood and rate of widening are specific. Sometimes the segment loses its identity in outer wood due to loss of the primary ray. Tracheid size is constant and of no diagnostic value. Pitting, however, is a fundamental character and is the principal reason for making radial sections of wood. In most calamites the primary tracheids are annular and scalariform, while secondary tracheids may be scalariform, reticulate, or pitted. Usually calamites have one type of pitting in secondary wood or a quick change from scalariform to pitted near the pith; but rarely a scattered mixture of the three types occurs in one stem. Previous authors have expressed doubt about the diagnostic value of pitting because of this occasional mixture of pitting types and the fact that the interface between tracheids and secondary ray cells is covered with scattered simple pits. Such detail is usually blurred in petrified calamitean stems, and it is difficult to tell simple pits from bordered pits. In any radial section there are likely to be tracheid walls exposed that lie against ray cells. Areas of simple pits so exposed may be found on a tracheid of *Arthropitys communis* known to have scalariform tracheids only. An area free of ray cells should be selected for study of pitting to avoid this difficulty.

Secondary rays may be specific because of their relative frequency, the length of cells, and whether they are simple or compound. Increased frequency and multiseriate conditions in outer wood occur in the same stem; hence, tangential sections from inner wood and outer wood should be made to obtain a true picture of ray conditions. Radial sections show better the height of ray cells.

VII. *Interfascicular Segment or Primary Ray.*—Although synonymy of these two terms is here implied, the primary ray carries a more restricted meaning; in calamite literature it is that part of the interfascicular segment made up of parenchyma.

The interfascicular segment is the most variable tissue in calamite steles and is used as a fundamental diagnostic character. Indeed, generic separation is based largely upon it. It is interesting to note that *Calamodendron* and *Arthroxylon,* with segments composed of prosenchyma flanking primary rays and solid prosenchyma respectively, are specialized. Variation in such segments is so small, even on a theoretical basis, that very few species in these two genera have been described, and it is likely that there will be very few more in the future for this reason. On the other hand, the fact that *Arthropitys* has a large number of species may perhaps be due to the fact that it has an unspecialized segment starting from the pith with a band of homogeneous parenchyma that may vary considerably. Williamson and Scott (1895) outlined the variability of interfascicular segments, which was later refined by Knoell (1935) to include variation of the primary ray in *Arthropitys.* This outline appears as follows.

1. Primary ray persists in secondary wood.
    a. Primary ray remains constant in width.
    b. Primary ray gradually becomes narrow.
2. Primary ray does not persist in secondary wood.
    c. Primary ray disappears abruptly with onset of cambial activity.
    d. Primary ray disappears somewhere in secondary wood.
        (1) Proportion of ray parenchyma in interfascicular wood then becomes equal to that in fascicular wood.
        (2) Proportion of ray parenchyma in interfascicular wood becomes greater than that in fascicular wood.

Of interest are the several ways by which rays diminish or disappear within secondary wood. They have been summarized in essence by Knoell as follows:

1. Tapering due to decrease in cell size or cell row number.
2. Tapering due to insertion of new tracheid rows at margin.
3. Tapering due to replacement of ray cells by tracheids in flanking rows.
4. Disintegration due to insertion of new tracheid rows between median rows.
5. Disintegration due to replacement of ray cells by tracheids in median rows.

One or more of these factors operate in any species and should be noted in a description.

Tangential sections show best the vertical extension of primary ray cells, which is of diagnostic value. Also supra- and infra-nodal canals appear in this view as swellings at each end of a ray. When tissue is present, it is irregular, isometric parenchyma. The infra-nodal canal is the larger of the two, making it possible to orient the direction of the axis. In some stem species canals are not prominent, but in others they persist as hollow structures even after the primary ray has disappeared, and are real "canals."

The bulk of the collection used in this investigation consisted of some 70 odd stem fragments. Most of them are from three localities: West Mineral, Kansas; Berryville, Illinois; and Booneville, Indiana. A few specimens are from several localities in Iowa, Illinois, and Indiana. Most specimens belong to the genus *Arthropitys*. There are several specimens of *Arthroxylon*, chiefly from Iowa, but none of *Calamodendron*. A few specimens fall into species of European material and a considerable number into American species already described.

ARTHROPITYS **illinoensis** Anderson, sp. nov.

This species is based on eight specimens collected from Berryville, Nashville, Freeburg, and Dix, Illinois. All stems are decorticated and are of three size classes. Three are hardly more than twigs, with pith diameters ranging from .6 to 1.1 cm. and total diameters from .9 to 1.4 cm. Four are intermediate with pith cavities and total diameters varying from 2.2 to 3.0 cm. and 4.1 to 6.5 cm., respectively. The largest stem is unusual in that its pith (diameter 6.5 cm.) is surrounded by a sheath of secondary wood only .5 cm. thick. It is apparently the remains of a young major axis fossilized before much secondary wood had formed and presumably before the axis had elongated much beyond this level.

Cross-sectional views (pl. 20, fig. 3) show that pith tissue is preserved between fascicular segments only. The segments themselves are wide, spaced nearly 2 mm. apart, and characteristically blunt at the inner edge. Circular protoxylem canals are relatively large, ranging from 175 to 250 μ in diameter. The primary ray disappears quickly, its parenchymatous cells being replaced by tracheids soon after initiation of cambial activity. Fascicular segments merge into a homogeneous sheath of secondary wood interspersed with secondary rays. A tangential section cut fairly near the pith (fig. 7) shows alternate wood sectors and primary rays. Ray cells are elongate vertically and may reach 300 μ in height. Near the nodes rays enlarge at both ends into the nodal canals formed of irregularly packed, isometric cells. Within an internode secondary rays are sparse and hard to see because they are uniseriate and composed of elongate cells, 100–300 μ tall, separated by slanting cross walls. Within a nodal region secondary rays are numerous and multiseriate. Figure 5 is a radial section showing rays cut in various sections. Here the elongation of ray cells is more apparent. Tracheids have three to four rows of alternate bordered pits.

The type specimen is of special interest since there are three roots attached to it which appear to be referable to *Astromyelon Williamsonis* (Cash and Hick) Williamson. These decorticated roots are about 1.5 cm. across. Broad, blunt, fascicular segments with prominent central secondary rays, large centripetal tracheids, uniform fascicular and interfascicular wood, so characteristic of *A. Williamsonis,* are easily observed. The segments originate from the innermost wood of the stem and at the same level as leaf traces. The pith cavity enlarges gradually in its outward course, and toward the inside there seem to be peripheral "canals" which are really small groups of large, thin-walled cells, giving the root primordium a stem-like appearance; they disappear farther out. The course of the root is perpendicular to the stem axis for about 1 cm.; then it gradually bends downward at a 30 degree angle upon emerging from the stem stele.

Diagnosis.—Decorticated stem 1–6.5 cm. in diameter, and internodes 1– several cm. long; pith cells usually absent; primary wood scarce, partially bordering a circular protoxylem canal 175–250 μ across; fascicular segment blunt at inner edge, broad and merging with others due to rapid loss of primary ray; tracheids with several rows of alternate oval pits; secondary rays sparse, uniseriate with elongate cells up to 300 μ tall, except at nodes where they are copious, multiseriate, and short-celled.

Type specimen: Coal ball no. 947, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: Berryville, Illinois; Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.

Other specimens and localities:

1. Coal ball nos. 860e, 948, 949, 950; Berryville, Illinois.
2. Coal ball no. 951; Freeburg, Illinois.
3. Coal ball no. 952; Nashville, Illinois.
4. Coal ball no. 953; Dix, Illinois.

ARTHROPITYS **versifoveata** Anderson, sp. nov.

Arthropitys sp. B. Andrews, in Ann. Mo. Bot. Gard. 39:189–218. 1952.

Andrews reported briefly on a large *Arthropitys* stem fragment from West Mineral, Kansas. Its poor preservation prevented a full description, and no specific name was assigned. Since then at least eight additional specimens of this stem have been collected from the Mineral locality, making possible a definite erection of a new species.

All the stems are decorticated and probably fragments from a major axis if not the primary axis, for their pith diameters range from 2.5 to 7.5 cm. and total diameters from 5 to 9 cm. Internodes vary with stem diameter and range from 1.2 to 3 cm. Of exceptional interest is the smallest stem (no. 956) which projects several centimeters beyond the end of the coal ball imbedding it, showing its nodes and branching habit. Nodes are spaced 1.2 cm. apart and each bears four branches 4 mm. thick and 90 degrees apart. Branches of one node alternate with those of adjacent nodes. That these structures are branches and not roots is proved by a tangential section showing them to arise somewhat above the level of leaf traces, as is characteristic of calamitean branches. It is therefore possible to place this species in the Cruciatus subgroup of the Eucalamites group of impression species.

Most of the pith is lost although it persists at the periphery and as pith disc remnants at nodes. Protoxylem canals are circular, varying from 150 to 200 μ across and are surrounded on three sides by primary tracheids (fig. 6). Each fascicular segment enlarges rapidly by insertion of new tracheid rows at the margin; thereafter it broadens very slowly toward the outside. Rather infrequently new rows of tracheids are inserted at the margin or middle of the ray, narrowing it or cutting it into two or more parts. In tangential section primary ray cells are nearly isometric, being elongated toward the margin (fig. 4).

Secondary tracheids have either scalariform or reticulate-bordered pitting (figs. 9 and 10). Both types are scattered at random throughout a stele and the proportion of each varies considerably among stems. So, while variation in proportion of pitting type is individual, the presence of this curious mixture is characteristic to this species along with a number of other features that are more constant. Secondary rays are made up of cells up to 200 μ tall. Rays are strictly uniseriate near the pith but may be biseriate farther out. Within nodal regions wood rays become more frequent and thicker.

This species is much like *A. kansana* Andrews with which it is usually found. Smaller primary wood groups, lack of strictly bordered pitting of tracheids or prominent biseriate rays are the chief characters that set it off from *A. kansana.*

Diagnosis.—Decorticated stem 5–9 cm. in diameter with internodes 1.2 to 3 cm. long; branches at every node alternating with those at adjacent nodes; protoxylem canal 150–200 μ across, surrounded on three sides by a relatively large amount of metaxylem; fascicular segment blunt, broadening very slowly and remaining distinct in outer wood; primary ray persisting as a band 4–6 cells wide, occasionally narrowed or split by insertion of new tracheid rows at margin or center; tracheids with scalariform or reticulate bordered pitting, both types scattered irregularly throughout the stem and in different proportions among stems; secondary rays of cells up to 200 μ high, uniseriate and sparsely biseriate in outer wood.

Type specimen: coal ball no. 829, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: West Mineral, Kansas; Fleming coal, upper Cherokee shale, Des Moines series; Middle Pennsylvanian.

Other specimens and locality: Coal ball nos. 754, 788, 826, 828, 954, 955, 956; West Mineral, Kansas.

ARTHROPITYS SP.

The following description is based upon a fragmentary specimen (coal ball no. 957) from New Delta, Illinois. Although it appears to be a new species it will not be given a species assignment because of its poor preservation and fragmentary condition. Only a sector of the stele is preserved showing a small part of the pith cavity surrounded by 2 cm. of secondary wood. Protoxylem canals are about 200 μ across and appear to abut directly onto the secondary wood. The fascicular segment is relatively narrow, ranging from .5 to 1.0 mm. passing toward the outermost secondary wood. The primary ray is about six cells wide and persists undiminished in the secondary wood (fig. 12). Secondary rays are uniseriate near the pith but farther out they are multiseriate and may be nearly as large as primary rays, giving the wood a somewhat uniform appearance in tangential view (fig. 8). Tracheids have three or four rows of circular pits on the radial walls. With its uniform primary ray and small pith cavity relative to thickness of secondary wood, this species resembles *A. bistriata,* but tracheids are pitted instead of scalariform as in this European species.

OTHER STEMS

There are two large stems (nos. 772 and 937) of *Arthropitys communis* from West Mineral, Kansas, that are very typical, with blunt, narrow fascicular segments, small protoxylem canals, scalariform tracheids and diminishing primary rays. Another specimen (no. 932) of this species is from Atlas Mine near Oskaloosa, Iowa. It is rather badly preserved, and this determination is tentative.

From Berryville, Illinois, several more specimens of *A. communis* var. *septata* Andrews have been collected (nos. 938–943), all of them remarkably alike, especially with 6–8 mm. internodes and septate tracheids of inner secondary wood. The status of this variety is more certain, because these characters which might seem questionable stand up statistically. Indeed, it can be suggested that this variety deserves specific status.

In a coal ball (no. 841) from Booneville, Indiana, there is a calamite stele with 9 cm. of secondary wood. Since only a sector of the stele is preserved, pith diameter is estimated to be 12 cm. From tangential sections it is seen that primary rays split into short, overlapping, multiseriate rays only slightly larger in outer wood than secondary rays, which also become multiseriate in outer wood. In the outermost wood there is a very high proportion of ray tissue and relatively few tracheids. Tracheids have alternate oval pits on their radial walls. By its size and anatomy this specimen is assigned to *Arthropitys gigas.*

Arthropitys Hirmeri Knoell is represented in a coal ball from Pinckneyville, Illinois (no. 568). It is a small stem with little secondary wood and has the characteristically abrupt loss of the primary rays immediately upon initiation of secondary growth.

From West Mineral, Kansas, there are six stems identified as *Arthropitys kansana* (nos. 750, 787, 789, 791, 830, 944). Also most stems (nos. 837, 838, 839, 840, 844, 877, 945) from Booneville, Indiana, are undoubtedly *A. kansana* despite the fact that their aspect is slightly different from the Kansas specimens. Upon careful comparison it is found that every character of the Booneville stems matches that of the West Mineral stems: general size, orientation of primary wood with pith and fascicular segments, protoxylem canal size of 250 μ, very slow diminution of the primary ray which is made up of small isometric cells, presence of biseriate rays in secondary wood, and several rows of alternate bordered pits on radial walls of tracheids. Their slightly different aspect is interpreted as an outcome of general difference in preservation of material between the two localities.

There is one Booneville specimen (no. 875) very similar to *A. kansana,* but it has scalariform pits on tracheids and ray cells tend to be elongated. The primary ray does not appear to diminish in the small amount of secondary wood present. This stem is tentatively assigned to *A. bistriata.*

Arthroxylon Williamsonii Reed is represented by three small stems, one (no. B-13) from Oskaloosa, Iowa, and the other two (nos. 933 and 936) from What Cheer, Iowa. A fourth stem (no. 946) comes from West Mineral, Kansas, and is unlike all stems previously described because of its large size. Pith diameter is 7.3 cm. and secondary wood is 2.3 cm. thick. It is identical with the *Arthroxylon* stem briefly reported by Andrews (1952). Like most West Mineral calamites it is fusainized from the pith cavity outward and highly pyritized from the outside in. Between pyritized and fusainized zones there is a small neutral band, the only hope for good study, suggesting that factors promoting formation of the two conditions are opposing and each tends to prevent the other from occurring. Primary wood and protoxylem canals can be seen, however, and are like those of *A. Williamsonii;* this specimen is probably a primary axis of this species. A tangential section through the well-preserved zone, cut about 1 cm. from the pith (fig. 13), shows that the fibrous zone does not contrast as sharply with the fascicular segment as in smaller stems. Another difference is the presence of a larger proportion of short-celled secondary rays, even in the fibrous zone, where they are absent in smaller stems. Such increase of ray parenchyma is probably in accordance with Bower's "size and form" principle and does not represent specific difference.

TWIGS AND LEAVES

Calamitean twigs are seldom found in coal balls although they are found as impressions in abundance. Williamson described some petrified twigs, and Hick (1894) gave a full treatment of them, noting their very close similarity to stems of *Equisetum.* Andrews (1952) briefly described two twig specimens probably identical to those described below. Isolated leaves are also infrequently found. Hick (1895) wrote a short account of them, but a more comprehensive treatment was made by Thomas (1911) who brought together scattered information about leaves and designated several specific types. In America only Hoskins (1928) and Reed (1938) have described petrified calamitean leaves.

In the present study the smallest stems found range from .7 to 3.0 mm. in diameter, forming a size class distinct from another class which ranges from 6 to 10 mm. The smaller class will be termed twigs in this paper, and the larger small stems. Only the twigs are definitely assigned to the new species erected below.

Calamites **rectangularis** Anderson, sp. nov.

This species is based on a large assemblage of shoots, isolated twigs and leaves in three coal balls from Berryville, Illinois.

In considering twig size, the diameter of the primary body (including distance across the pith plus primary wood) is more informative than total twig diameter. Since the cortex is somewhat uniform in thickness, complications of including secondary wood are thereby avoided and errors in measurement due to loss of phloem in preservation are minimized. Also, the distinction between twigs and stems is more apparent when the diameter of the primary body is used rather than total stem diameters. The primary bodies of 58 twigs measured varied from .2 to 1.0 mm. in diameter, with a median and mode of .6 mm. This variation shows a normal distribution; hence these twigs represent the highest order or ultimate branches of a calamite. The measurements show that these coal balls happened to preserve an ultimate branch system that is often preserved intact in an impression. For comparison, an impression of *Asterophyllites charaeformis* Sterenberg, taken at random, shows the last three degrees of branching. The largest axis is fragmentary and measures 4 mm. in diameter. The secondary axes are 1.5 mm. across at the base and .5 mm. near the tip, and the ultimate axes are .2 to .4 mm. across. The smallest part of the secondary axis is about as large as the largest ultimate branches, so it is possible that the fragments in the coal balls may represent two degrees of branching instead of one.

Leaves measure .3–.5 mm. in thickness, .5–.7 mm. in width, and 5–10 mm. in length. Thirteen leaves per whorl may be counted in one specimen (fig. 14), and other shoots appear to have about 12 per whorl. Variation in leaf size seems to be comparable to that in twig size. Figure 16 shows a representative longisectional view of a shoot.

The anatomy of a twig is typically calamitean, with a ring of fascicular segments, each with a protoxylem canal, unpreserved phloem, and primary cortex of two layers. The smallest twig is .6 mm. in diameter with a primary body .2 mm. thick. There are five fascicular segments and no secondary wood. A better-preserved specimen, shown in fig. 20, is slightly larger and 1 mm. in diameter; the primary body is .4 mm. thick, and has seven fascicular segments. The cortex is intact and there appear to be about twelve leaves per whorl. Twigs with a primary body approaching 1 mm. in diameter have 12 to 20 fascicular segments and may have up to .2 mm. of secondary wood (fig. 19). Otherwise they are quite similar to the smallest twigs.

As stated above, leaves seem to vary with their twigs in size. However, the larger leaves form a distinct class, sometimes being 1.5 × .8 mm. in cross-section but found closely associated with small stems about 6 mm. in diameter. Figure 15 shows cross-sections of leaves of both size classes that happen to be adjacent. The larger leaf is 1.5 × .6 mm. and the smaller is .7 × .4 mm. They are oriented in the same direction. Their cross-sectional shape is almost perfectly rectangular, quite unlike that of leaves previously described. There is a single layer of epidermis present, with some poorly defined stomata on the lower surface of the larger leaf. A palisade layer next underlies the surface and extends nearly around the central tissues. At the center there is a single strand of perhaps 20 tracheids. Phloem cells are probably not preserved. Surrounding the stele is the bundle sheath, which is proportionally larger than that in other species. Next to the stele, cells of the sheath are large and very thin-walled. Toward the outside they are smaller with thicker walls, and in longisectional view they appear fibrous. This fibrous zone is more pronounced on the upper side where it seems to form a sort of backbone for the leaf.

Diagnosis.—Shoot .7–3.0 mm. in diameter, bearing 12 leaves in whorls 1–5 mm. apart; axis calamitean with ring of fascicular segments each with a protoxylem canal and 2-layered cortex; leaves 5–10 mm. long and .3 × .5 to .8 × 1.5 mm. and of rectangular shape in cross-section, palisade layer and large bundle sheath surrounding single, unbranched vascular strand.

Type specimen: Coal ball no. 834, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: Berryville, Illinois; Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.

Other specimens and locality: Coal ball nos. 860, 879, 960; Berryville, Illinois.

The larger stem-size class ranges from 6 to 10 mm. in total width. Apart from being larger than twigs their organization is different. Primary wood groups and protoxylem canals are larger and more spaced out. Secondary wood is always present. Figure 18 shows a small stem about 6 mm. thick. There are 24 fascicular segments and .1 mm. of secondary wood. It seems evident, from comparing this stem with twigs one-fourth as large but with about the same number of fascicular segments, that the two represent different orders of branching. It is inconceivable that a twig could expand its width fourfold to become a small stem such as is figured. From this specimen and others scattered throughout the coal balls there can be seen a stelar organization similar to that of *Arthropitys illinoensis.* Configuration of the primary body and quick loss of the primary ray are partial evidence that the specimens belong to this species. It is further suggested that the twigs and leaves described above also belong to this stem species because of their close association with these small stems.

ROOTS

Petrified calamitean roots were first described in 1878 by Williamson, who assigned them the generic name *Astromyelon.* He found isolated fragments only and suspected that they might be stems somewhat allied to calamites. It remained for Renault and Zeiller (1890) to find them in organic connection with calamitean stems, confirming Renault's earlier hypothesis that they were roots of calamites. Renault also designated four of the five species of *Astromyelon* so far described. Anatomical descriptions were given by Renault, and by Williamson and Scott (1895a). Maslen (1905) wrote a masterly discussion of root-stem relationships.

During the present investigation isolated roots of various size were found, ranging from 2 mm. to several cm. in diameter. Although at least three size classes are represented, no very small roots have been observed of the type formerly called *Myriophylloides* with diarch or tetrarch protosteles and cortex with large intercellular spaces. In fact, no extra-xylary tissues were preserved in any roots observed. This assemblage appears rather varied anatomically, but some instances of branching make it possible to designate a small number of types.

Coal balls (nos. 840, 870, 872, 878, 947, 958) from Booneville and St. Wendells, Indiana, and Berryville, Illinois, were found to contain calamitean roots belonging to *Astromyelon Williamsonis.* The somewhat indistinct fascicular segments projecting only a little into the pith, quick replacement of interfascicular parenchyma by tracheids, a prominent secondary ray in the middle of each fascicular segment, and very large, thin-walled centripetal tracheids are characters that check point for point with described and illustrated specimens of this species from European coal balls. Such distinct characters are present only in root steles ranging from 4 to 10 mm. in diameter, roots of an intermediate order of branching. Associated steles of smaller size appear somewhat nondescript and similar to roots of this size belonging to other species.

ASTROMYELON **cauloides** Anderson, sp. nov.

This species is based on a number of roots found in coal balls from Berryville, Illinois, and St. Wendells, Indiana. All specimens are decorticated and their steles range from 2 mm. to several cm. in diameter, with a common anatomical configuration in all sizes except the very smallest which are nondescript.

The most characteristic features of this species in cross-sectional view are the rather pointed fascicular wedges accentuated by the presence of considerable interfascicular parenchyma. In a segment, centripetal metaxylem is reasonably well-developed and projects into the nearly intact pith, giving a distinct point to a segment. Wood rays are mostly uniseriate. The primary ray is lost through replacement of parenchymatous cells by tracheids in a radial row of cells plus the insertion of new rows of tracheids. There is considerable variation in the rate of ray loss; smaller roots and some larger ones lose their primary rays almost as soon as production of secondary wood begins (fig. 17), while in others the ray persists through 4 mm. of secondary wood (fig. 1). The writer does not believe that such variation constitutes specific difference, since all other characters are constant, especially the manner of ray loss, and there is a continuous series of ray-loss rates among the observed specimens.

This root most closely resembles *Astromyelon augustodunense* Renault, in which the primary ray persists considerably into secondary wood. In this species, however, ray loss is accomplished by a decrease in ray row number only. There is no replacement of parenchymatous cells by tracheids, and the outer tracheidal row of a fascicular segment flanking a ray in the inner wood remains as the flanking row until it meets, in outer secondary wood, a flanking tracheidal row of the next segment. Figure 2 is a tangential section near the pith showing primary rays and wood sectors. Cells of primary rays are large and somewhat elongate (75–300 μ), as well as those in the uniseriate secondary rays scattered among tracheids. Pitting on radial walls of tracheids is strictly scalariform.

In its anatomical organization this root appears more like a stem than the other root species. It is further suggested that it belongs to *Arthropitys communis* var. *septata* on the basis of association in coal balls and such anatomical details as elongate ray cells and scalriform pitting.

Diagnosis.—Decorticated root 2–40 mm. in diameter; pith nearly intact and of thin-walled parenchyma; primary xylem mesarch with protoxylem poles at periphery of pith, no protoxylem canals present; secondary fascicular wood with scalariform tracheids and 1–2 seriate rays 2 to many cells deep; ray cells up to 300 μ deep; interfascicular segment with a varying amount of primary ray lost through replacement of parenchymatous cells by tracheids in a given row plus insertion of new tracheid rows.

Type specimen: Coal ball no. 853, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: Berryville, Illinois; Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.

Other specimens and localities:

1. Coal ball nos. 882, 887, 929, 930, 931; Berryville, Illinois.
2. Coal ball nos. 925, 926, 927; St. Wendells, Indiana.

ASTROMYELON **pluriradiatum** Anderson, sp. nov.

This species is based upon a single specimen in a coal ball from Berryville, Illinois. It most closely resembles *Astromyelon reticulatum* Renault, which is figured showing very broad fascicular segments similar to those in this new root. However, the small amount of secondary wood in Renault's specimen makes precise comparison impossible. The stele is decorticated, the pith cavity is 6 mm. in diameter, and there are 7 mm. of secondary wood. Figure 21 shows a cross-section that happens to cut a branch root in its outward course; outside the main axis it has a diameter of 1 cm. and organization similar to that of the parent root.

The chief characteristic of this root is its high proportion of ray tissue in secondary wood. This is apparent even in cross-section where a very prominent 3- to 4-seriate ray appears centrally in each fascicular segment. In tangential view the high proportion of ray parenchyma (fig. 11) makes the wood appear almost herbaceous. Rays are 1- to 4-seriate and the largest may be over 1 cm. deep.

Multi-seriate rays form an overlapping network of parenchymatous tissue in the center of a fascicular segment, a condition opposite to that in calamitean stems and most roots where the interfascicular segment is more parenchymatous. Ray cells are little elongated, being rather isometric in multiseriate rays; their depth ranges from 50 to 150 μ.

The pith cavity is nearly hollow with tissue only at the periphery. Fascicular segments are very broad and blunt due to a small amount of primary wood, immediate succession of secondary growth, and rapid insertion of new tracheidal rows in each segment. A radial section through a protoxylem pole shows annular tracheids of protoxylem and a few scalariform tracheids of centrifugal metaxylem. Cells of the centripetal xylem are pitted and seem to be transitional to parenchyma, for they are shorter, have thinner walls and squared end-walls. Secondary tracheids have either single rows of elongate pits or 3–4 rows of alternating oval pits and are up to 50 × 60 μ in cross-section. Primary rays lose their identity quickly through rapid tapering and replacement of parenchymatous cells by tracheids in any given cell row.

Diagnosis.—Decorticated root 2 cm. in diameter with connected branch root 1 cm. thick; pith 6 mm. across, hollow, with peripheral parenchyma only; primary xylem mesarch with 12 protoxylem poles at periphery of pith; centripetal metaxylem of thin-walled, short, square-ended tracheids; fascicular segments very broad and blunt facing the pith; secondary wood with high proportion of ray parenchyma, especially in center of fascicular segment where there are up to 4-seriate rays; ray cells 50–150 μ deep; secondary tracheids to 50 × 60 μ in cross-section with single rows of elongate pits or several rows of alternate oval pits; primary ray lost through replacement of parenchymatous cells by tracheids in a given radial row of cells.

Type specimen: Coal ball no. 959, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: Berryville, Illinois; Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.

CONES

In the thirty-odd years in which coal balls have been cut and studied in America, calamitean cones have very rarely been discovered in them. Some of the earlier workers listed their occasional presence, but to date there have been no descriptions of them, although several paleobotanists are currently working on such cones and papers should be soon forthcoming. The present investigation covers nine cone specimens, eight of which belong to one species. All of them are assignable to *Palaeostachya* owing to adaxial insertion of sporangiophores. One of the cones is about 2 cm. in diameter while another is at least 3 cm. in diameter. None of the *Palaeostachya* species described from petrifactions comes close to approaching this size, and, of impression species, only *P. arborescens* Sternberg and *P. Schimperiana* Weiss are in this size class, being 3 and 2.5 cm. in diameter respectively (Weiss, 1876, 1884). Correlation of these impression species with the new petrified cones is ruled out, since *P. arborescens* has about 20 bracts per whorl while the corresponding petrified cone has from 40 to 60; and *P. Schimperiana* has an axis 1 cm. thick while the petrified cone has one about 4 mm. thick.

Palaeostachya **multifolia** (Reed) Anderson, comb. nov.

Calamites multifolia Reed, in Bot. Gaz. 100:324–335. 1938.

This species is based upon six specimens in coal balls from Berryville, Illinois, and two in a single coal ball from Booneville, Indiana. The complete cone is at least 8 cm. long and 3 cm. wide. Toward the base it narrows to 1.5 cm., the tapered zone being sterile. Nodes are spaced 3 to 4 mm. apart and bear 40–60 whorled leaves fused at their bases. Sporangiophores arise obliquely from bract axils and bear four pendant sporangia. This species is heterosporous.

At the very base the axis is small and consists of xylem only. The primary body is 2 mm. in diameter and secondary wood is .5 mm. thick making the total diameter 3 mm. In cross-section it is perhaps indistinguishable from a stele of a vegetative twig (fig. 22). A few scattered bracts are present at this level. The stele then enlarges to its full width of 6 mm. in a distance of 2 cm. A cross-sectional view of the widened axis shows a somewhat different organization than that below. The stele is crushed to an elliptical shape, and loosely surrounding cortex is present. There are now 26 fascicular segments in contrast to 18 at the level below. Segments show a tendency to group into pairs and there are .3 mm. of secondary wood. The uppermost cross-section of the axis shows it to be the same size, but with very little secondary wood, and a very pronounced tendency for the segments to group in pairs (fig. 24). There are now 30 fascicular segments. Since there is very little secondary wood at this level, the cone probably does not extend much farther. A tangential section through the stele gives proof that bracts of one whorl are superposed on those of the whorl below. At most nodes fascicular segments of the internodes above and below stand directly in line with each other. Only a few show alternation at nodes, marking the insertion of new segments into the stele. Hence, most leaf traces and their bracts arise directly above each other.

The bracts of a whorl number from 40 to 60 in the widest part of the cone and are fused basally into a lateral disc. This disc is very well shown in the specimen from coal ball no. 858 (fig. 25). When a small piece of the cone was accidentally broken off, the top surface of a whorl of fused bracts was exposed. One-fourth of the whorl contains 10 bracts, so the whorl must contain 40. This whorl is near the base of the cone and does not have the maximum number of bracts possible. From the photograph it can be seen that the bracts are fused into a basin-like disc, with the mid-portion of each bract ridged somewhat. The disc dips down a little before bending up sharply to a rim where the bracts separate. Cells composing the disc are rather elongate with walls of moderate thickness. This tissue persists into the upturned free bract, forming a sort of "backbone" which gradually disappears. At the rim of the disc on its lower surface the lamina of each bract projects abruptly, extending down as much as 3 mm., where it practically touches the disc below nearly enclosing the sporangia (fig. 23). Any cross-section cuts the free bract tips at several levels since the tips overlap four nodes above before terminating (fig. 24). Innermost is the disc cut on the bias; next the upturned disc is still fused but with the lamina of each bract added; the next outer whorl shows free bracts without disc tissue; and the outermost whorl shows a small, nondescript bract tip. There is some sort of imbricate pattern of the bracts, but since they are superposed, the pattern must be due to local displacement of free tips.

Sporangiophores arise in bract axils, traverse an oblique course upwards (fig. 26), flatten out and bear 4 sporangia (fig. 27). Figure 24 is a cross-section of the cone on a 30-degree slope, which shows sporangia from a somewhat tangential view. The number of radial rows of sporangia approximately equals the number of bracts, and there is one sporangiophore for every two radial rows of sporangia. Thus it is inferred that the number of sporangiophores is one-half that of the number of bracts. At this level the axis has 30 fascicular segments, each of which presumably gives off one sporangiophore as in other *Palaeostachya* species described by Renault (1882) and Hickling (1907). Hence, there must be about 60 bracts per whorl at this level, which cuts through this cone at its full width. Whether sporangiophores alternate or are superposed on bracts cannot be determined. Sporangia fill most of the space between whorls of bracts and must have been 5 × 2 × 2 mm. in size. The wall is made of a single layer of cells which are somewhat elongated in surface view.

This species is heterosporous. Microspores and megaspores have spherical shape; their walls are thin, psilate and tend to fold; and the triradiate mark is small—all of these characters placing them in the genus *Calamospora* Schopf, Wilson & Bentall (1944). In coal ball no. 839 only microspores are found, which measure from 60 to 80 μ in diameter. The type cone in coal ball no. 860 has microspores of the same size (fig. 28), and in one spot near the tip are some scattered megaspores 180 μ in diameter (fig. 29). In the cones from coal balls nos. 882 and 858 only megaspores are present (fig. 30), and they are badly shattered so that isolation is impossible. These megaspores vary from 250 to 280 μ in diameter. In no. 882 are associated structures that may be microspores, but owing to poor preservation it is not possible to observe definite spore characters.

As Hartung (1933) has pointed out, heterospory in the calamites is rather frequent. Indeed, this family shows more incipient heterospory than any other in the plant kingdom in terms of relative frequency and the fact that microspores and megaspores never differ as much in size as do those in other heterosporous groups. Considering such observed frequency, it is puzzling that the calamites did not reach the "seed" habit as did the lepidodendroids. Apparently *Palaeostachya multifolia* was a species in a transition to heterospory, for the only specimen giving positive evidence of heterospory in the same cone has megaspores considerably smaller than those in cones containing megaspores only, assuming that the latter are true megasporangiate cones having reached the limit of heterospory observed in the calamites.

Coal ball no. 961 contains a cone that is notable because its developing apex is preserved. The length of the whole shoot is about 10 cm. Organization of the axis and bracts places it clearly within this species even though there is no trace of any sporangia. There are some associated structures that might be spores, but they do not possess definite spore characters. This specimen checks point for point with *Calamites multifolia* Reed, and since it is a developing shoot, as is Reed's, its identity is evident. Total size, presence of forty leaves per whorl fused basally into a disc, bract size, shape, and organization are features in common. There is also grouping of fascicular segments into pairs, which Reed noted as a feature of *Palaeostachya vera* Seward. Therefore, it seems apparent that Reed's twig is a developing cone in which sporangia were not yet developed or destroyed in fossilization.

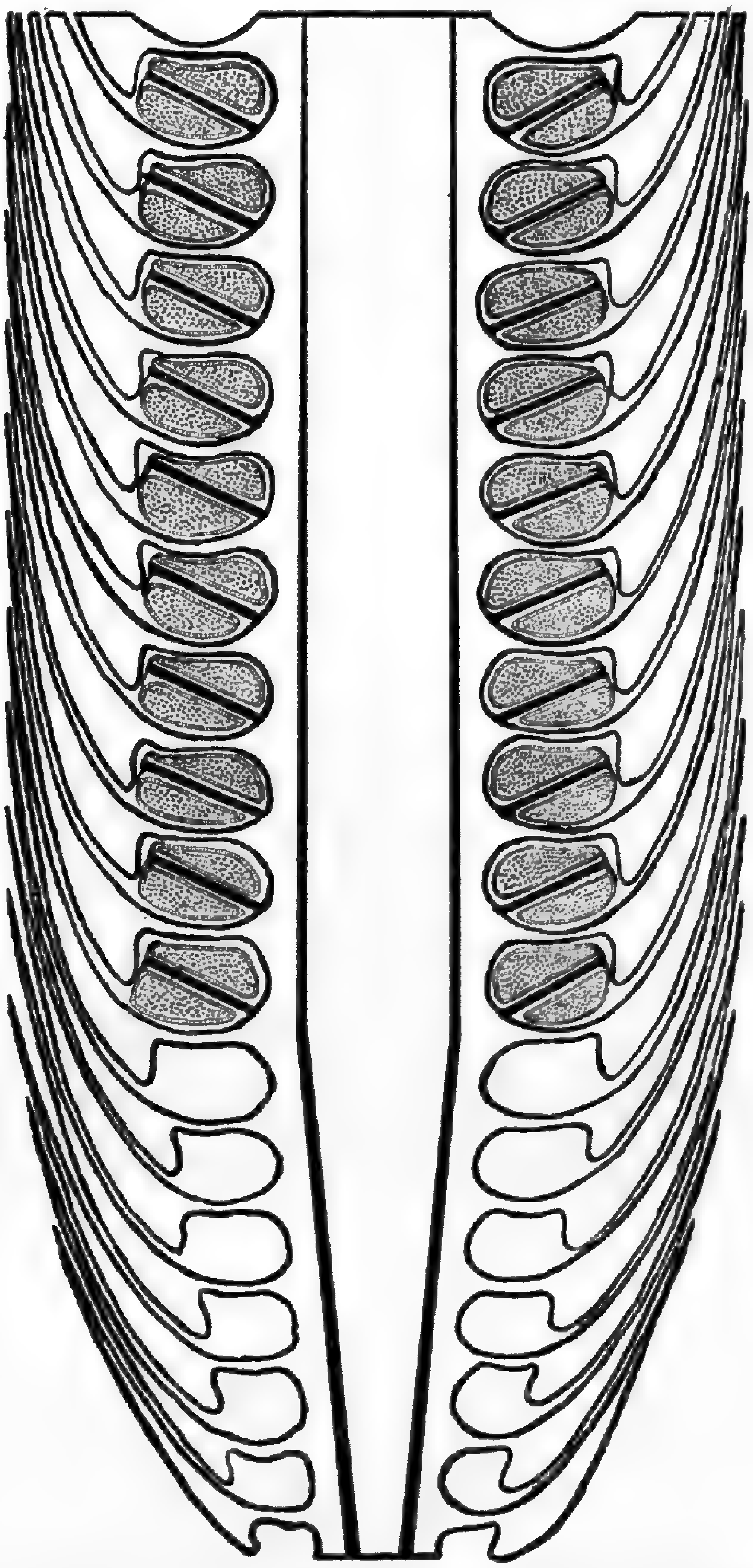
The meristem itself is worthy of note since so few are known in paleobotany. The first peel to show the shoot apex reveals no less than 11 surrounding whorls of leaves in various developmental stages (fig. 31). Cells of the apex are isometric, about 30 μ in diameter, and show a tendency to periclinal division toward the shoot margin. Immediately below this region the tissue appears to be crushed from one side; but 1 mm. below the apex this distortion disappears, the shoot has nearly reached full width, a hollow pith cavity has formed, and even vascular tissue has begun to differentiate. Such a blunt apex is very similar to that of *Equisetum*. Further development shows that once primary xylem is formed, its position or distance from the shoot center does not change with the addition of secondary wood. A problem arises in accounting for the difference between the number of fascicular segments and the number of bracts at a given node. In this species there are about 30 segments and 40 bracts per whorl. In calamites there is usually one leaf trace given off per segment, but favorable sections of this cone show three traces developing from some pairs of fascicular segments. In this way an appropriate increase in leaf trace and bract number occurs.

Since all the specimens are shattered or fragmentary, a drawing is appended to give a better visual impression of the morphology and proportions of this cone (text-fig. 1).

Diagnosis.—Cone 8 cm. long and 3 cm. wide, tapering to 1.5 cm. near the base; axis 1 cm. wide with hollow pith cavity, 30 fascicular segments grouped in pairs, each with protoxylem canal and secondary wood; bracts 40–60, whorled at nodes and fused into a lateral disc around the axis, and with tips upturned, free and 1.5 cm. long; sporangiophores 30 at node, inserted at level of upper bract surface, and bearing 4 pendant sporangia; heterosporous with microspores 60–80 μ and megaspores 190 to 280 μ in diameter; spores of genus *Calamospora*.

Type specimen: Coal ball no. 860, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: Berryville, Illinois; Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.



Text-fig. 1. Longitudinal reconstruction of *Palaeostachya multifolia* based upon specimen in coal ball no. 860, × 2.

Other specimens and localities:

1. Coal ball nos. 834, 843, 858, 961; Berryville, Illinois.
2. Coal ball no. 839; Booneville, Indiana.

PALAEOSTACHYA SP.

The following description is based upon a single specimen in a coal ball from What Cheer, Iowa. Its structures are obscured considerably by pyrite, and most tissue appears partly decomposed. Strangely, cortical tissues are present while most of the tracheids have disappeared. The cone is 5 cm. long and 2 cm. wide. Its axis is 5 mm. in diameter, rather slender for a cone as large as this, and is set with whorls of 24 bracts spaced 4.5 mm. apart. In three nodes studied, 14 sporangiophores arise somewhat above and between the bracts. One sporangiophore presumably develops from one fascicular segment of the main axis and terminates in a fleshy, cruciate structure bearing 4 sporangia. Sporangia contain microspores 75–100 μ in diameter belonging to the genus *Calamospora.*

A point of interest is the relationship between number of bracts and of sporangiophores at a node. In this specimen 24 bracts and 14 sporangiophores are counted at each node. Also sporangiophores seem to come off the axis in pairs, probably a consequence of their parent segments in the main axis being grouped in pairs. In several observed instances each sporangiophore of a "pair" is placed on each side of a given bract. This further complicates the picture so that no possible symmetrical arrangement of 24 bracts and 14 sporangiophores at a node can be devised. It follows that no exact relationship exists between bract and sporangiophore number; thus tending to support Hickling's (1907) theory that sporangiophores belong to a separate node that moved downward phyletically to coincide with the bracteate node. It was also observed that sporangiophore number is controlled by fascicular segment number (one segment gives off one sporangiophore) while bract number is not rigidly controlled by segment number, as demonstrated in *P. multifolia,* thus accounting for the independence of bract and sporangiophore number.

STRATIGRAPHIC CORRELATIONS

While there have been stratigraphic correlations of plant impression fossils, made chiefly in Europe, very little work has been done with petrified plant remains found in coal balls. Schopf (1941) compared horizons of various American coal ball localities with each other and with European coal ball horizons as a background for his stratigraphic discussion of *Mazocarpon.* To date no general stratigraphic correlation of megafossil species has been prepared which would supplement spore studies in solving stratigraphic and floristic problems of past ages. If the paleobotanists studying coal balls could cooperate in a publication giving the results of their researches, a general picture of vertical and horizontal distribution of megafossil species might be obtained. The following is a very meagre contribution toward this end, involving only petrified calamitean species described in this investigation and those reported by Andrews (1952).

Calamitean remains were recovered from the following coal ball localities, all of which occur in Middle or Upper Pennsylvanian deposits.

1. What Cheer, Iowa; Des Moines series.
2. Atlas Mine, near Oskaloosa, Iowa; Des Moines series.
3. Argus Mine, near Oskaloosa, Iowa; Des Moines series.
4. West Mineral, Kansas; Fleming coal, Cherokee shale, Des Moines series.
5. Red Ray Mine, Freeburg, Illinois; No. 6 coal, Carbondale group.
6. Pyramid Mine, Pinckneyville, Illinois; No. 6 coal, Carbondale group.
7. New Delta, Illinois; No. 6 coal, Carbondale group.

8. Nashville, Illinois; No. 6 coal, Carbondale group.
9. Dix, Illinois; Calhoun coal, McLeansboro group.
10. Berryville, Illinois; Calhoun coal, McLeansboro group.
11. Booneville, Indiana; Petersburg coal No. 5, Petersburg series.
12. St. Wendells, Indiana; near Parker coal, Conemaugh series.

Species and their localities are listed below:

Arthropitys communis: West Mineral, Berryville and Atlas Mine. This species has a considerable vertical distribution comparable to that in Europe.

Arthropitys communis var. *septata:* Berryville.

Arthropitys gigas: Booneville. This horizon is considerably below that of European horizons, uppermost Carboniferous and lowermost Permian, from which this species has been reported.

Arthropitys bistriata: Booneville. Conditions here as with *A. gigas.*

Arthropitys Hirmeri: Pinckneyville. This horizon is somewhat above the Katharina deposits of the Ruhr from which this species was first reported.

Arthroxylon Williamsonii: What Cheer, Argus Mine, and West Mineral. These localities are probably near the same level and above the Lower Coal Measures of England from which this species was reported earlier.

Astromyelon Williamsonis: Berryville and St. Wendells. These localities are near the same level and much higher than the Lower Coal Measures of England from which this species was first reported.

Astromyelon cauloides: Berryville and St. Wendells.

Astromyelon pluriradiatum: Berryville.

Arthropitys illinoensis: Berryville, Red Ray, Dix and Nashville. This species appears to have a reasonably wide vertical distribution but so far is confined to central Illinois.

Arthropitys versifoveata: West Mineral.

Arthropitys kansana: West Mineral and Booneville. Booneville is somewhat above West Mineral stratigraphically and several hundred miles away, giving this species a wide distribution.

Calamites rectangularis: Berryville.

Palaeostachya multifolia: Berryville, Booneville and Harrisburg, Indiana (Reed). This cone species has some vertical distribution, and the Booneville locality is at the same level as Harrisburg, from which Reed recovered a vegetative base of this cone.

ACKNOWLEDGMENTS

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EXPLANATION OF PLATE 20

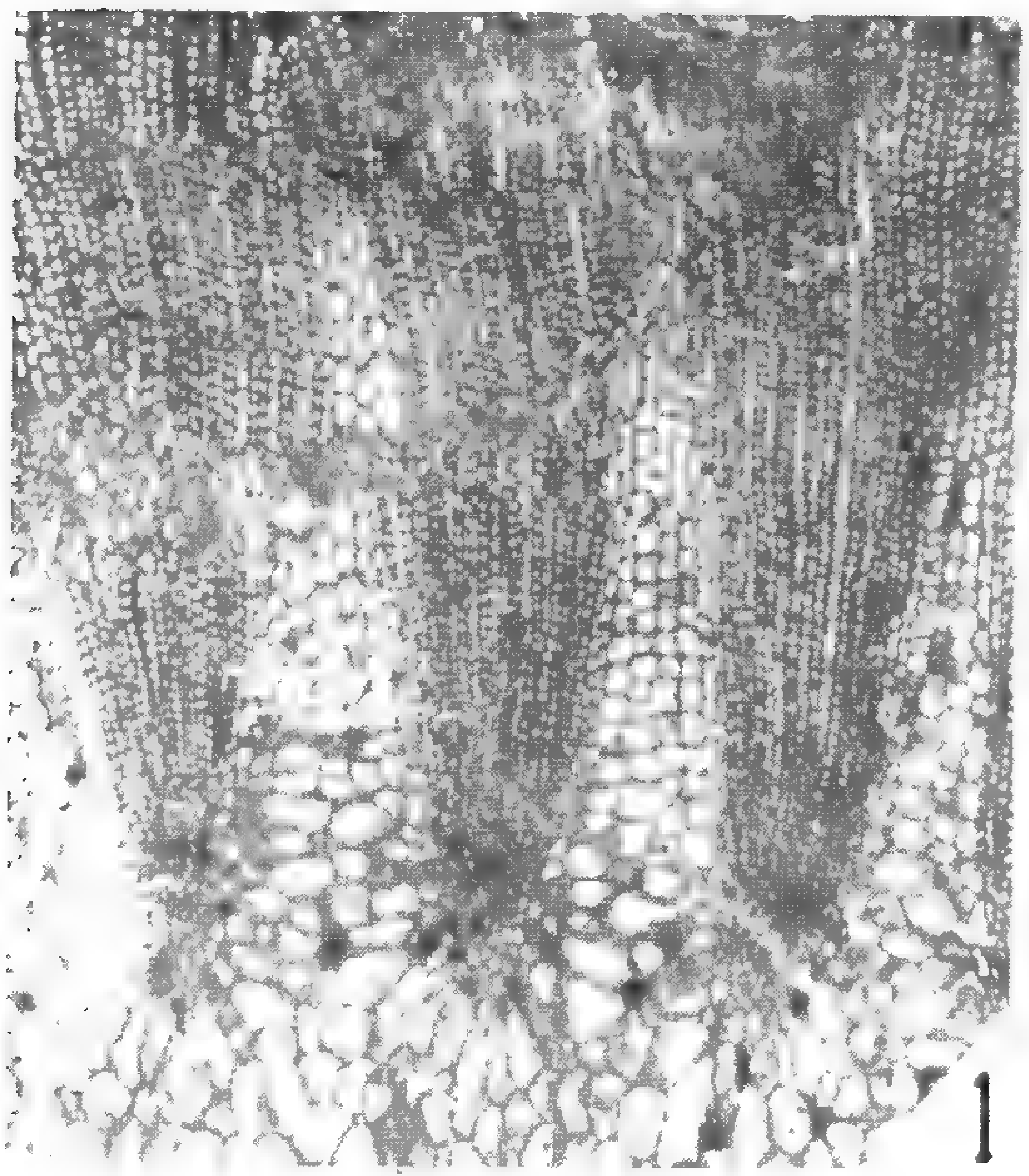
Figs. 1 and 2. *Astromyelon cauloides* Anderson: Fig. 1. Cross-section of portion of large root. Coal ball no. 853. Peel 853. × 14; fig. 2. Tangential section of wood near pith showing wood sector and primary rays. Coal ball no. 853. Slide 2360. × 28.

Fig. 3. *Arthropitys illinoensis* Anderson. Cross-section of inner wood portion. Coal ball no. 947. Peel 947. × 12.

Fig. 4. *Arthropitys versifoveata* Anderson. Tangential section of wood showing wood sector and primary rays. Coal ball no. 829. Slide 2356. × 31.

Fig. 5. *Arthropitys illinoensis.* Radial section of wood showing secondary ray cells and tracheids. Coal ball no. 947. Slide 2358. × 75.

Fig. 6. *Arthropitys versifoveata.* Cross-section of inner wood portion. Coal ball no. 829. Peel 829. ×14.



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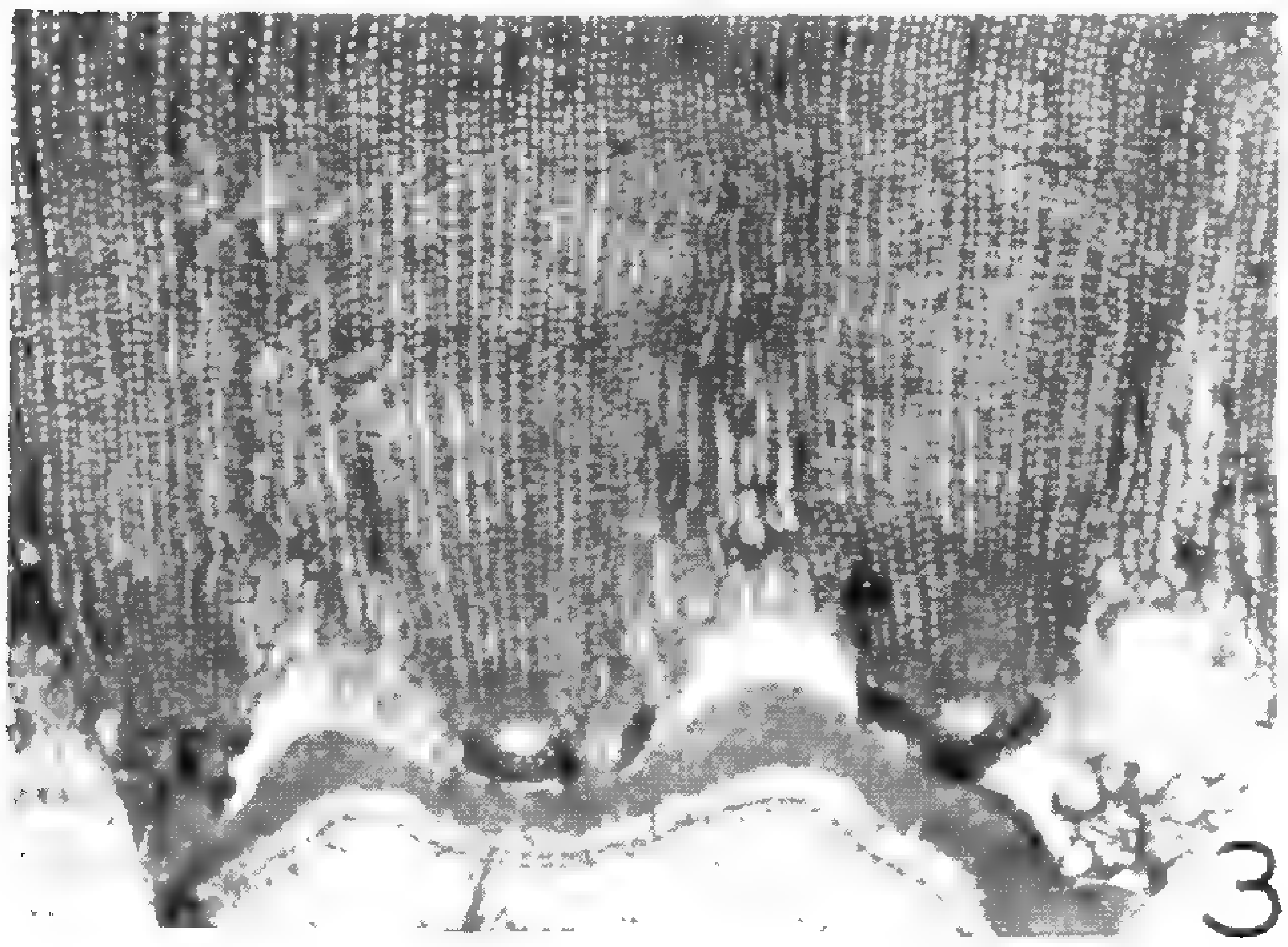

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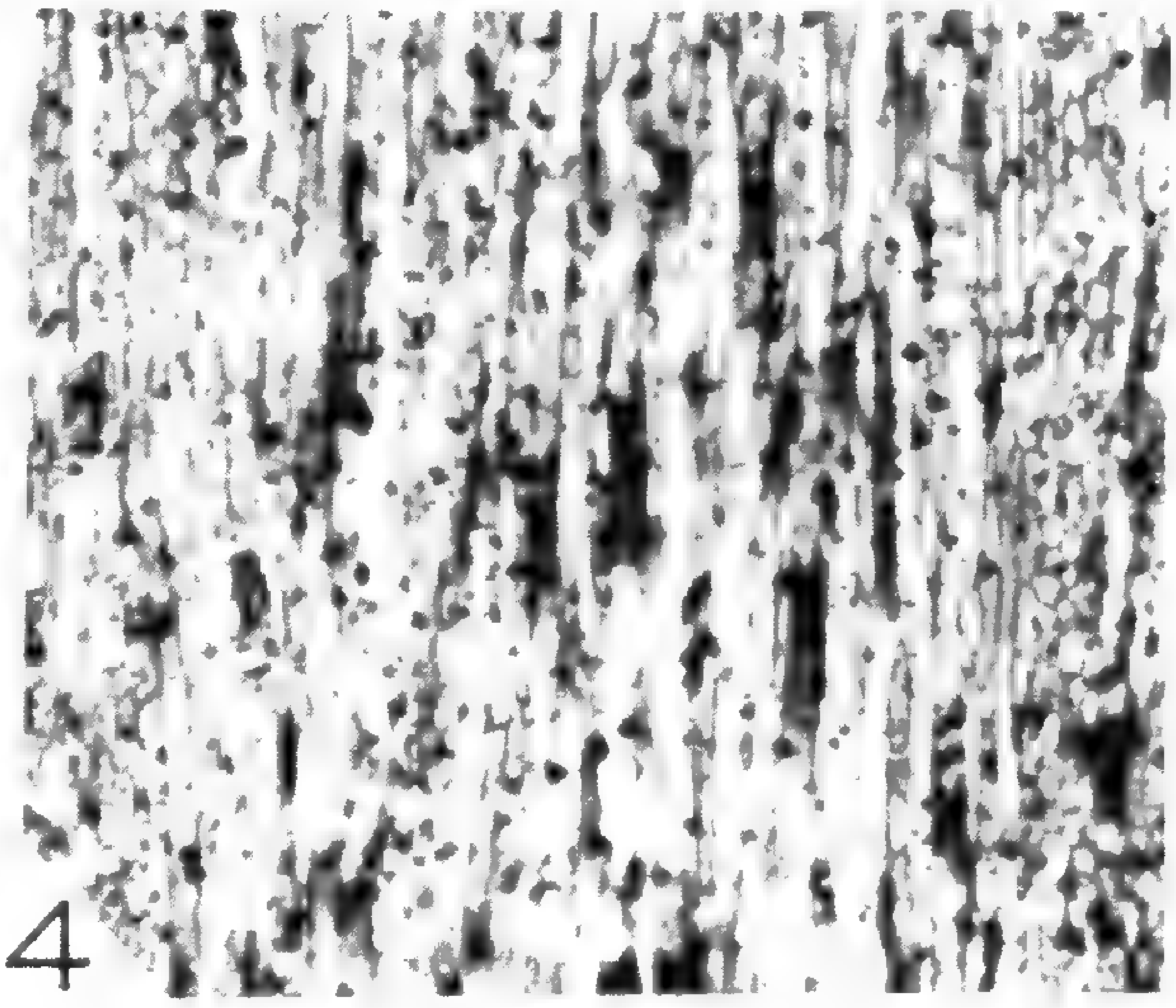

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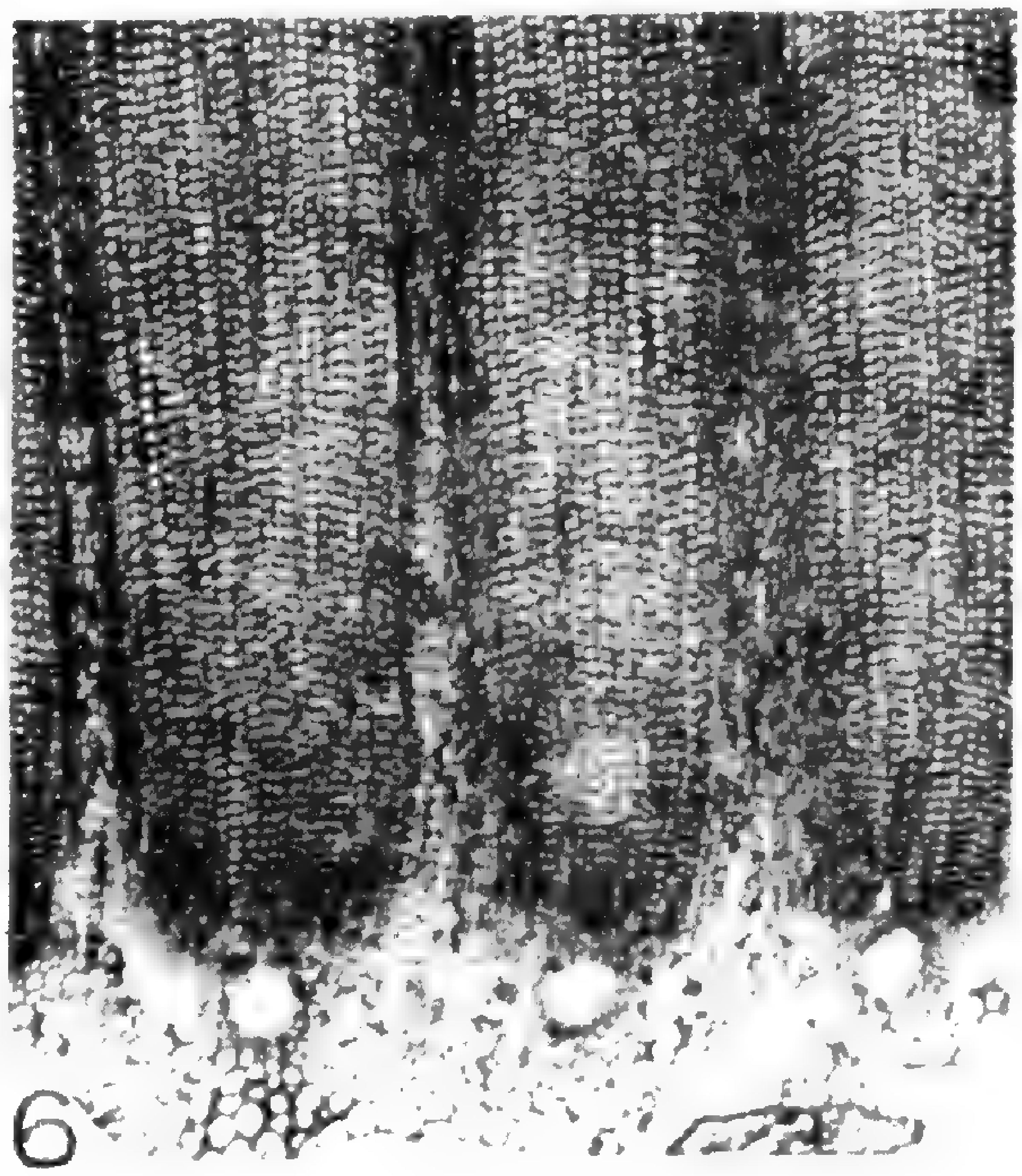

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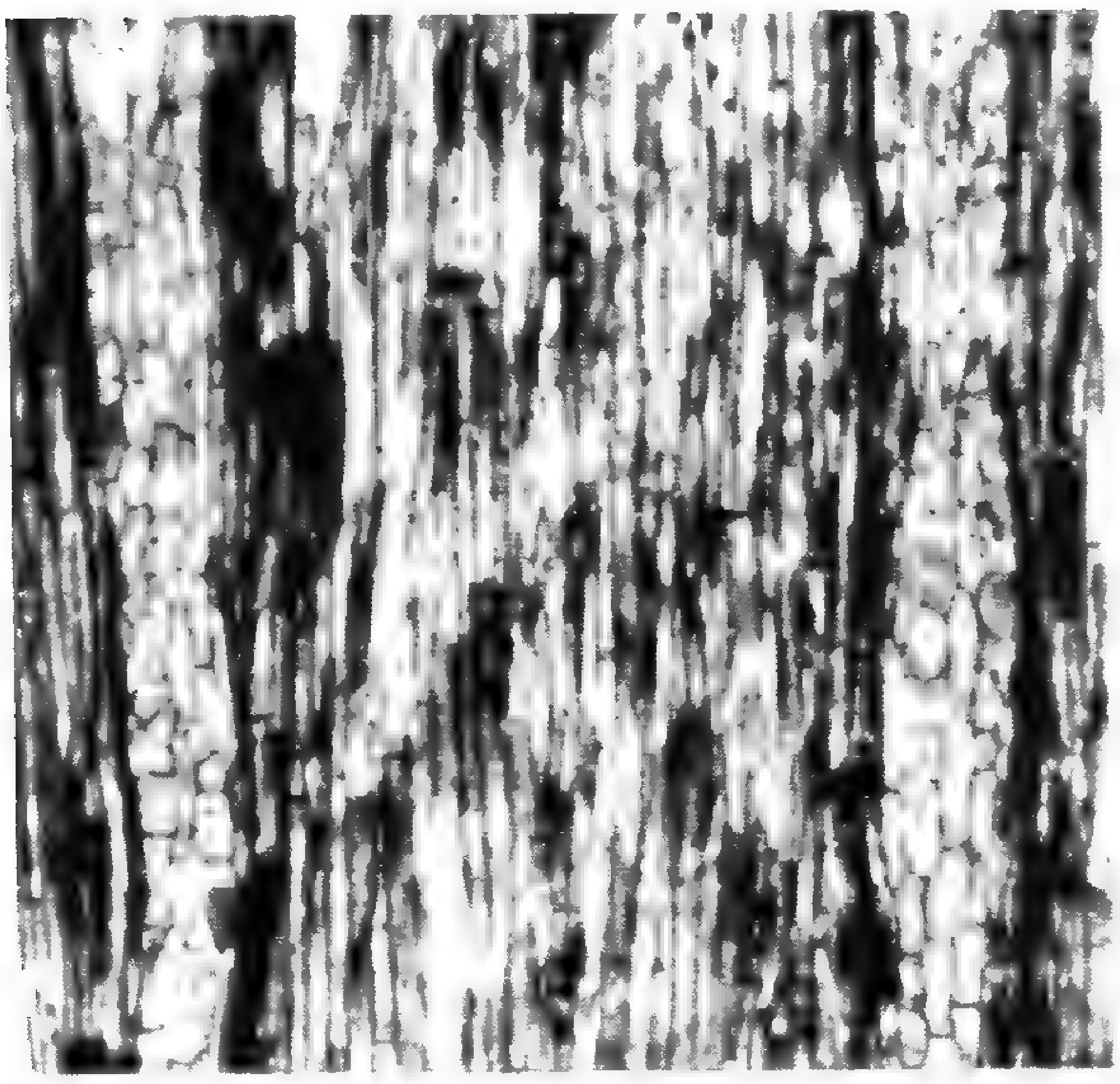
ANDERSON—AMERICAN PETRIFIED CALAMITES



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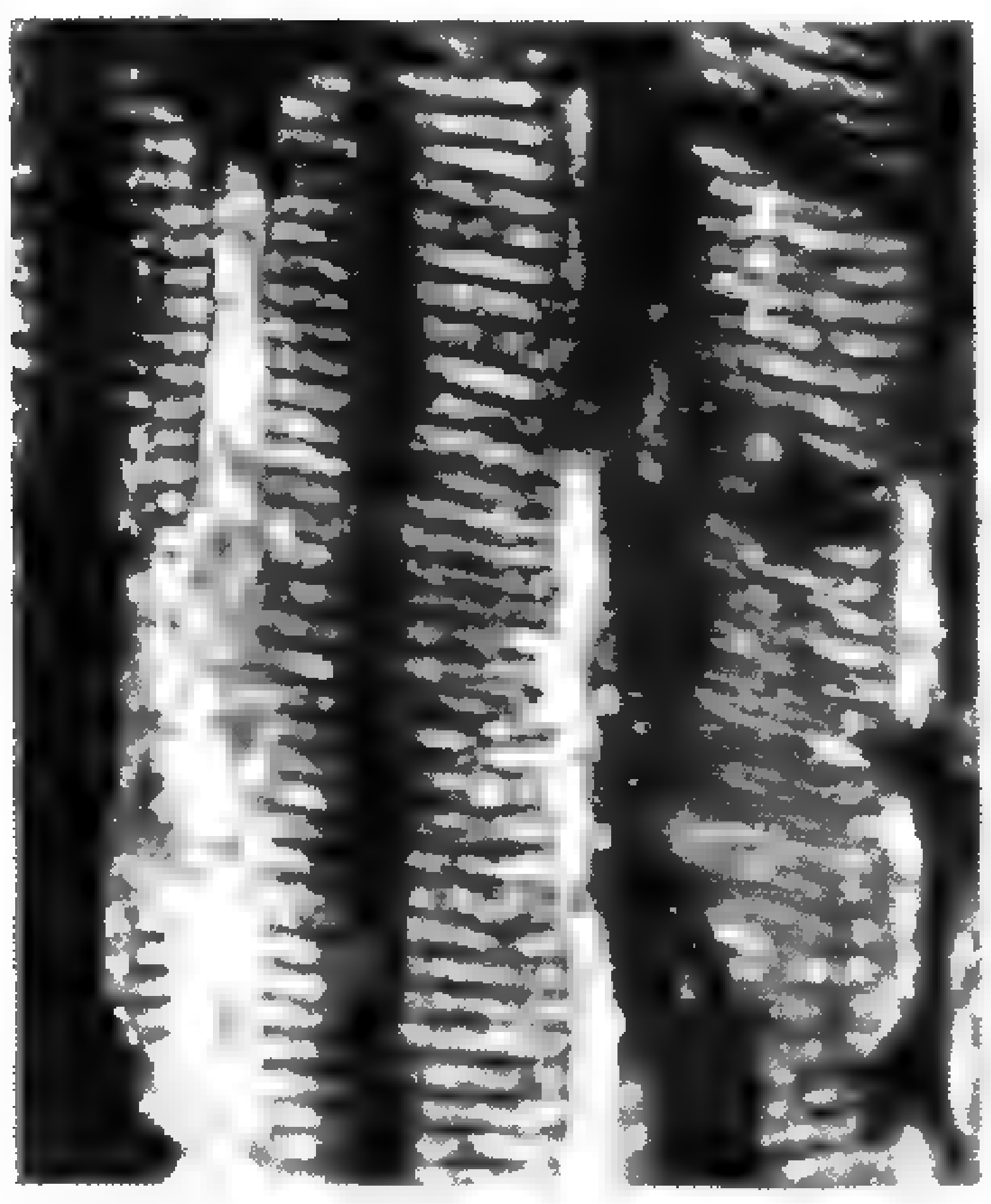

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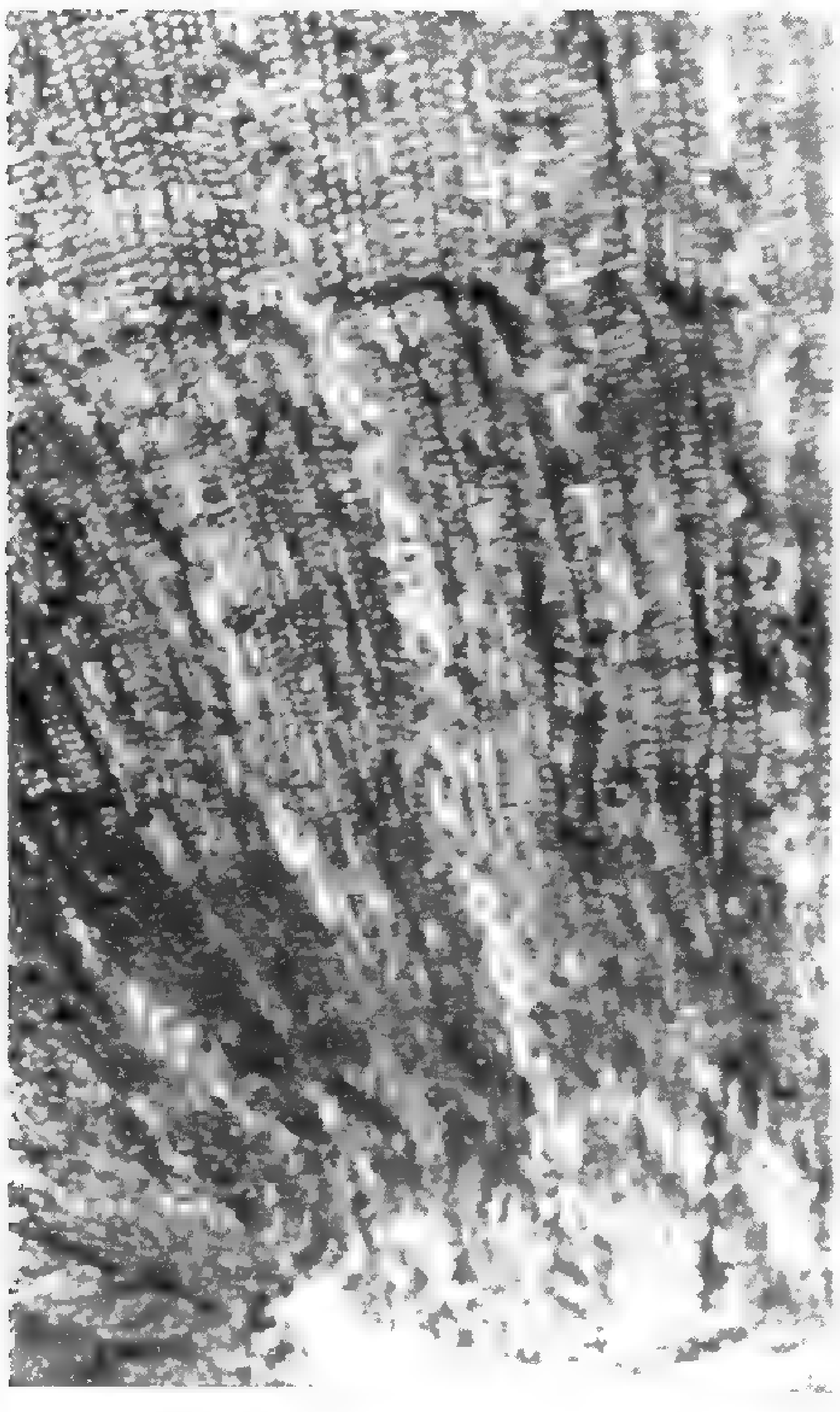

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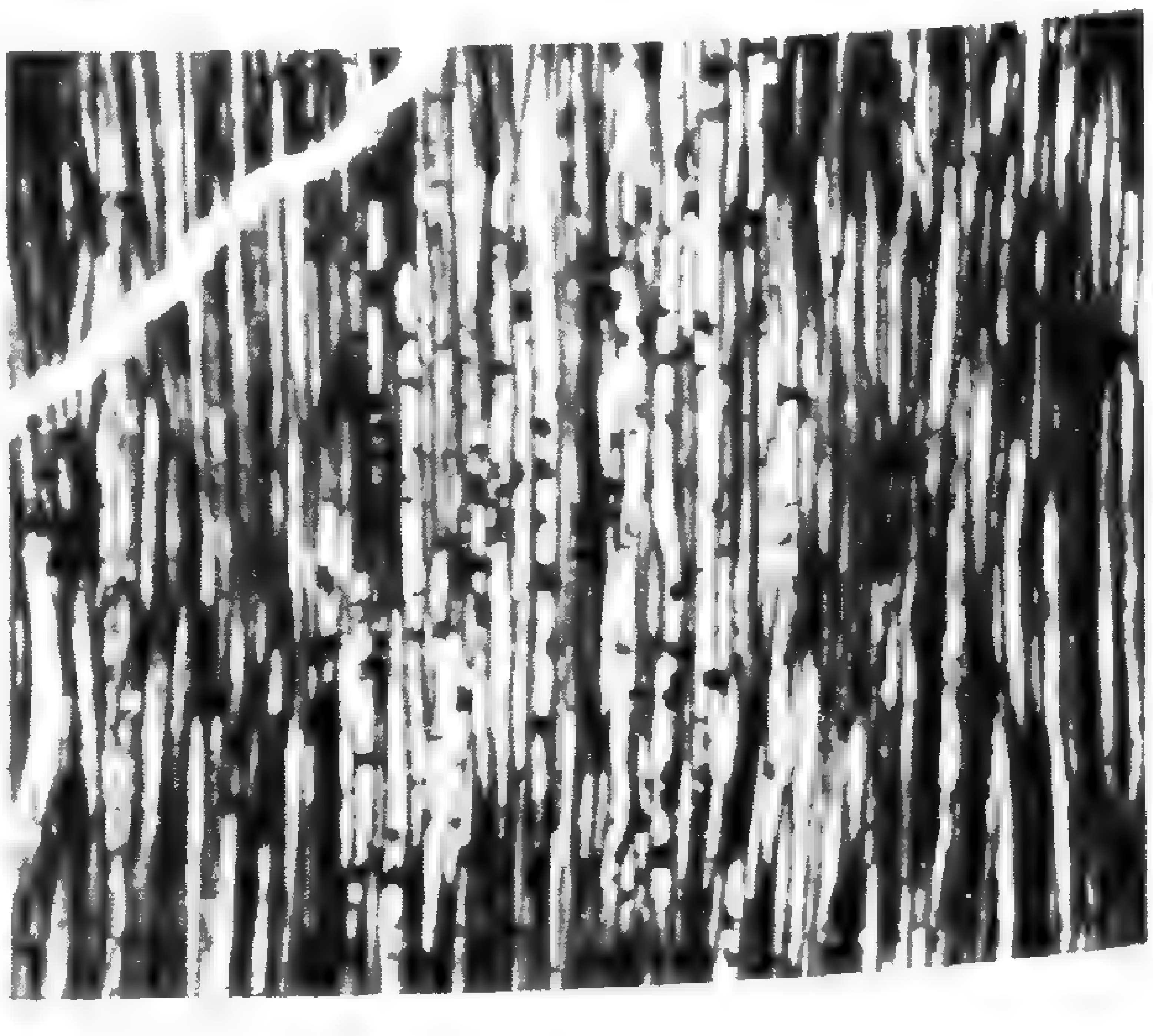

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ANDERSON—AMERICAN PETRIFIED CALAMITES

EXPLANATION OF PLATE 21

Fig. 7. *Arthropitys illinoensis* Anderson. Tangential section of wood near the pith showing wood sector and primary rays. Coal ball no. 947. Slide 2357. × 28.

Fig. 8. *Arthropitys* sp. Tangential section of outer wood showing tracheids, primary rays and a large secondary ray. Coal ball no. 957. Slide 2359. × 33.

Figs. 9 and 10. *Arthropitys versifoveata* Anderson. Pitting in radial walls of tracheids. Coal ball no. 753. Slide 1924. × 133.

Fig. 11. *Astromyelon pluriradiatum* Anderson. Tangential section of wood. Coal ball no. 959. Slide 2363. × 28.

Fig. 12. *Arthropitys* sp. Cross-section of wood portion showing sectors and undiminishing primary rays. Coal ball no. 957. Peel 957. × 11.

Fig. 13. *Arthroxylon Williamsonii* Reed. Tangential section of wood showing short-celled secondary rays in woody and fibrous zones. Coal ball no. 946. Slide 2354. × 16.

EXPLANATION OF PLATE 22

Calamites rectangularis Anderson (except fig. 17)

Fig. 14. Nodal cross-section near apex of shoot showing departure of whorled leaves. Coal ball no. 834. Slide 2366. × 42.

Fig. 15. Cross-sections of leaves. Coal ball no. 860. Slide 2368. × 39.

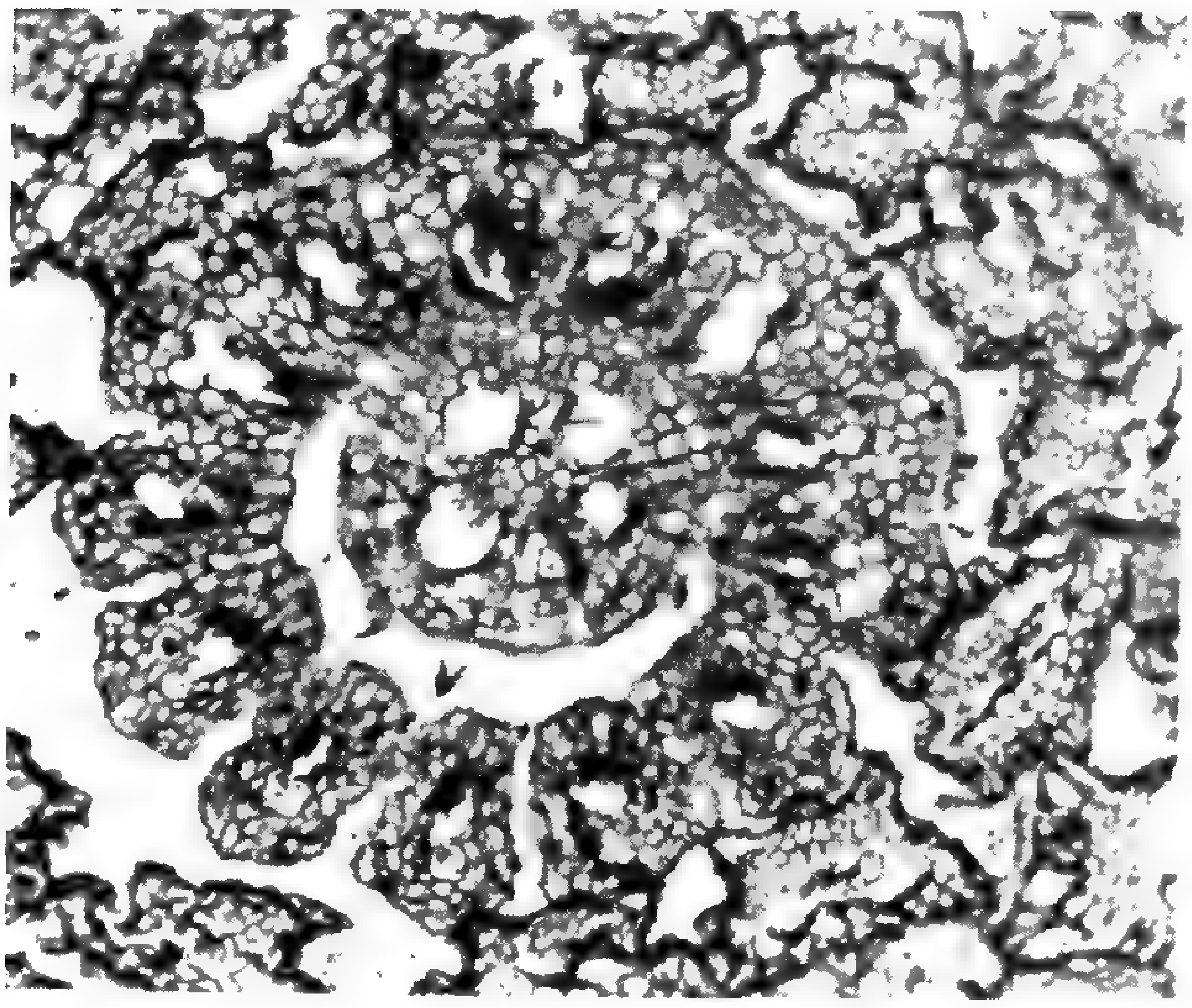
Fig. 16. Longisection of shoot. Coal ball no. 879. Peel 879A-tan 11. × 6.

Fig. 17. *Astromyelon cauloides* Anderson. Cross-section of small root. Coal ball no. 882. Peel 882A. × 7.

Fig. 18. Cross-section of small stem. Coal ball no. 860. Peel 860J-t1. × 11.

Fig. 19. Cross-section of large twig. Coal ball no. 860. Slide 2367. × 21.

Fig. 20. Cross-section of small twig. Coal ball no. 960. Slide 2364. × 44.



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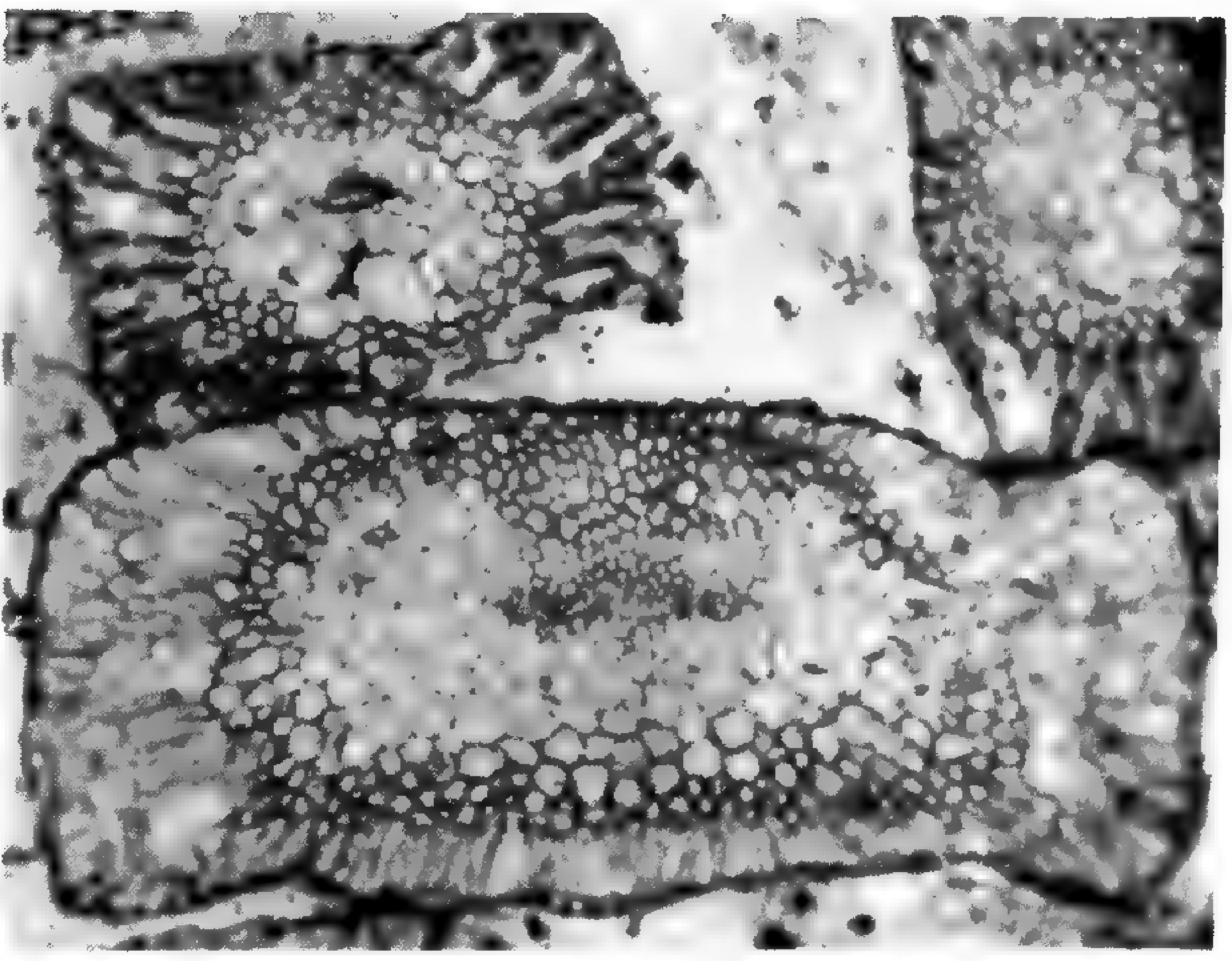

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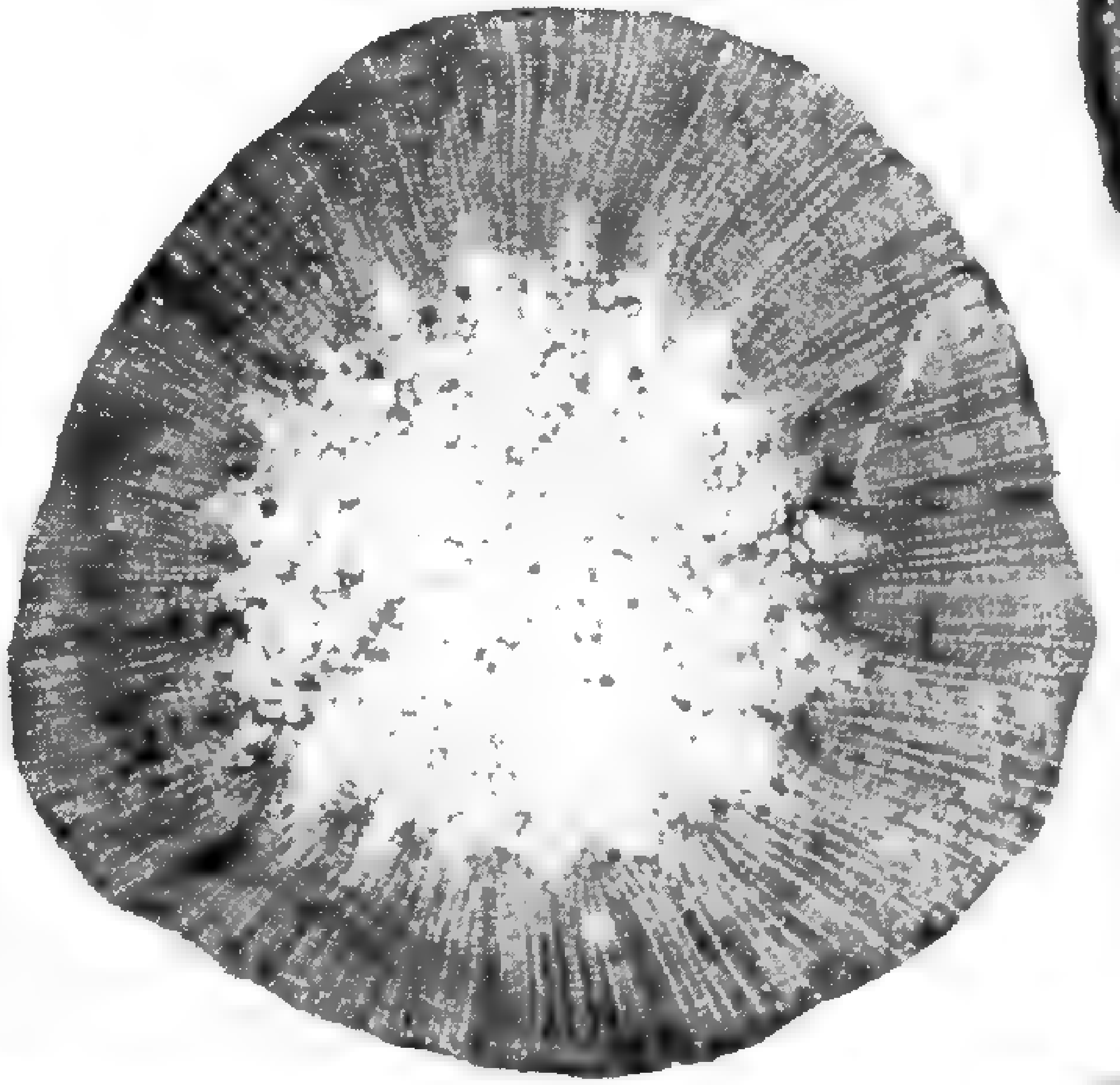

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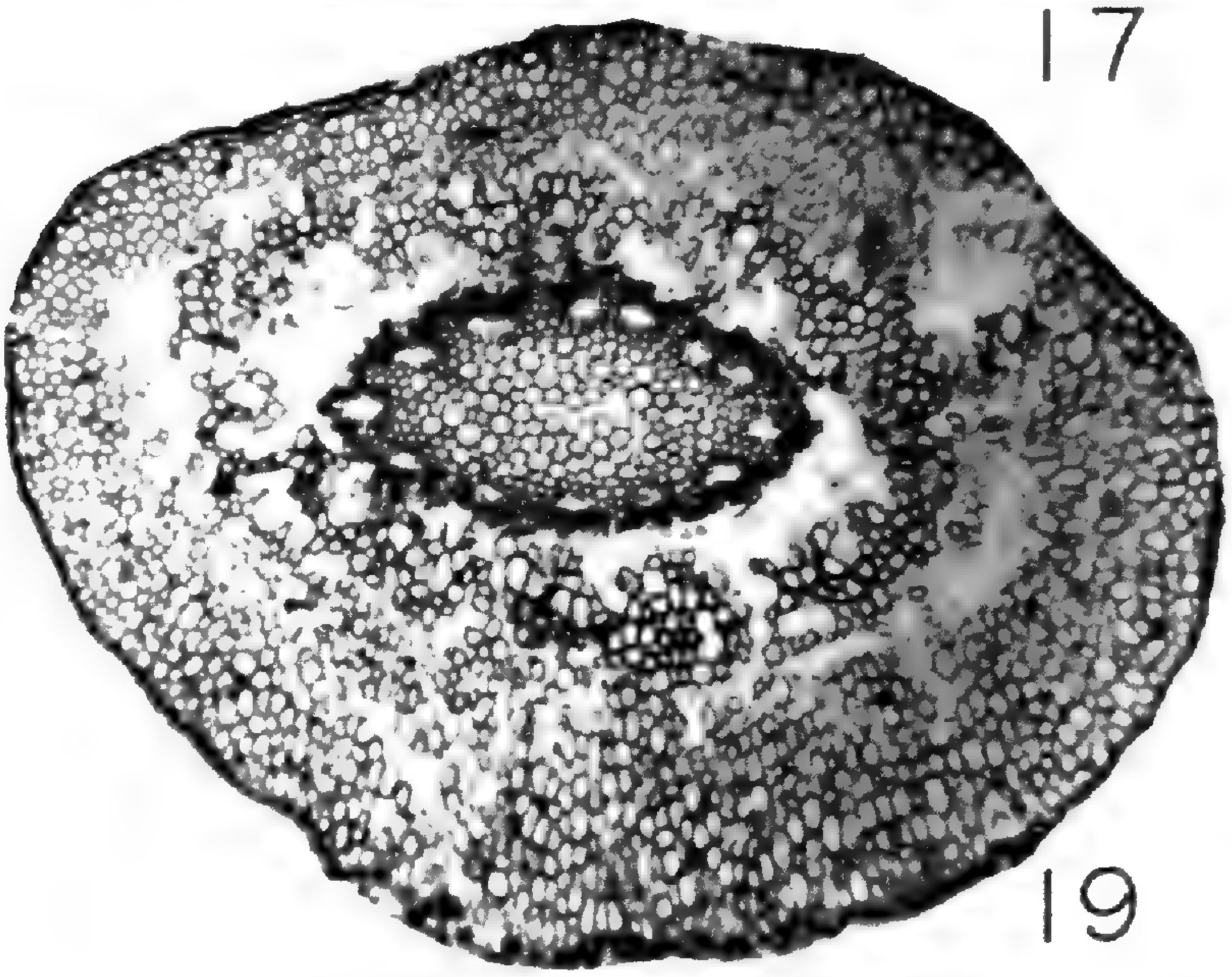

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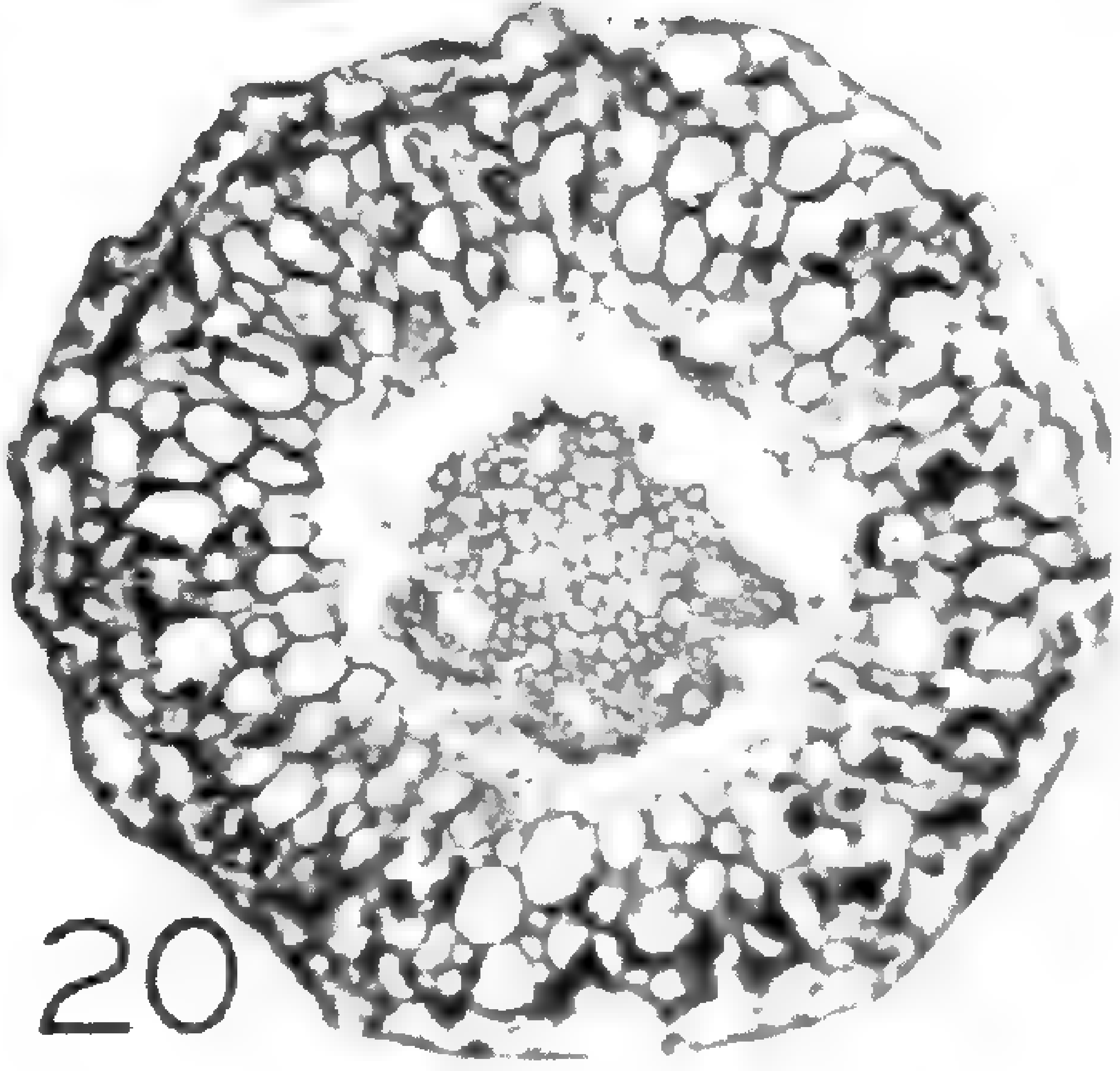

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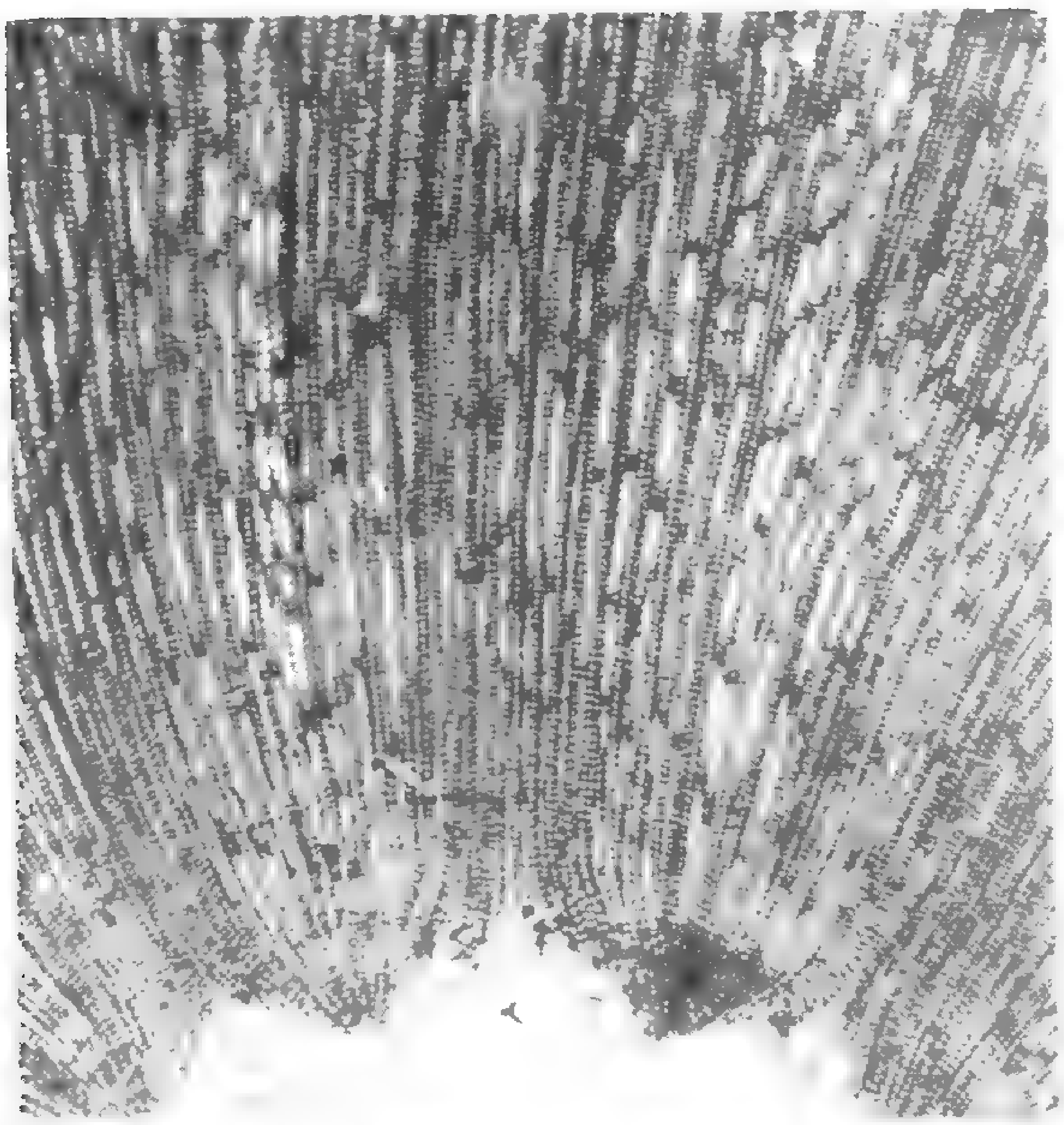
ANDERSON—AMERICAN PETRIFIED CALAMITES



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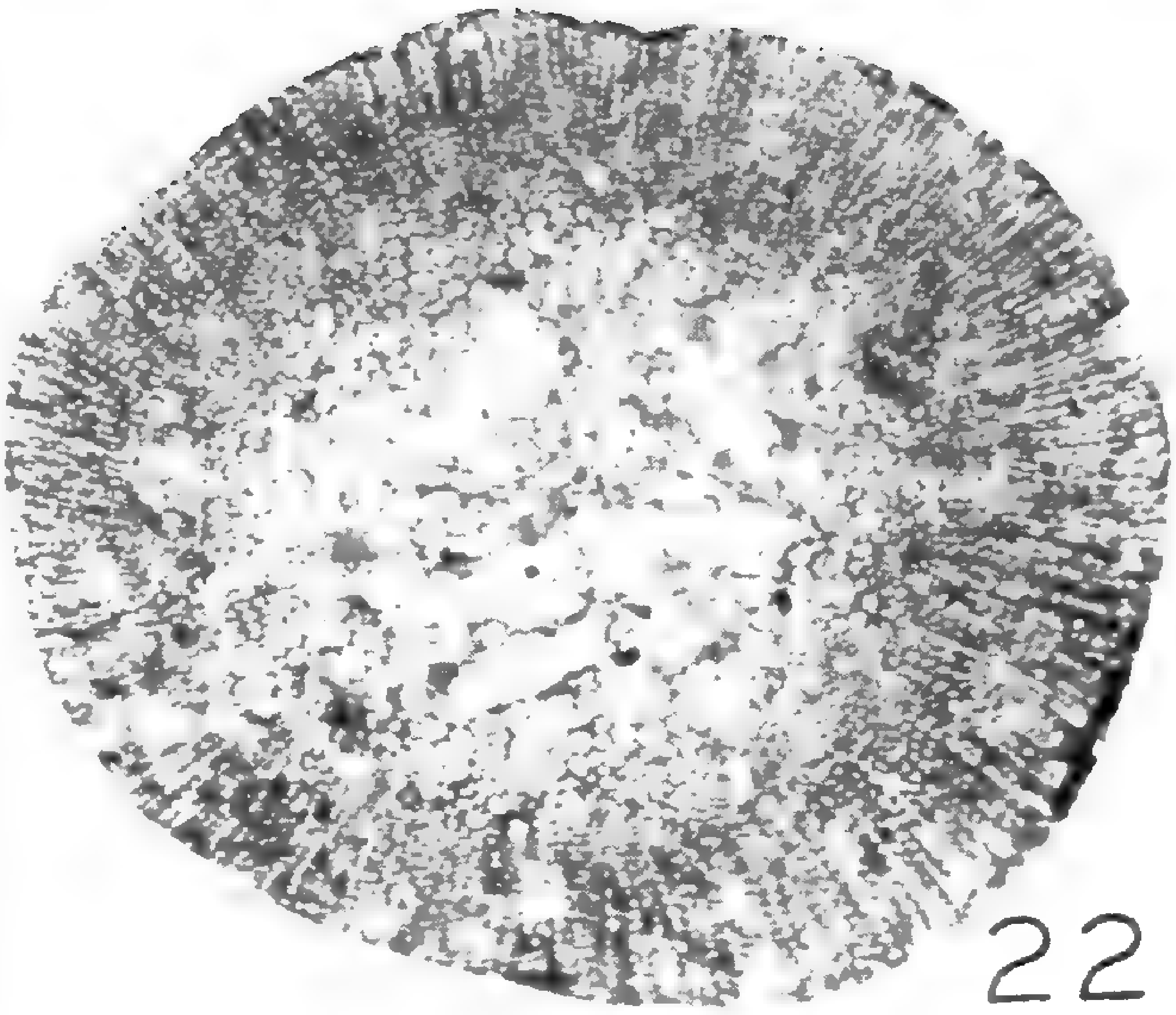

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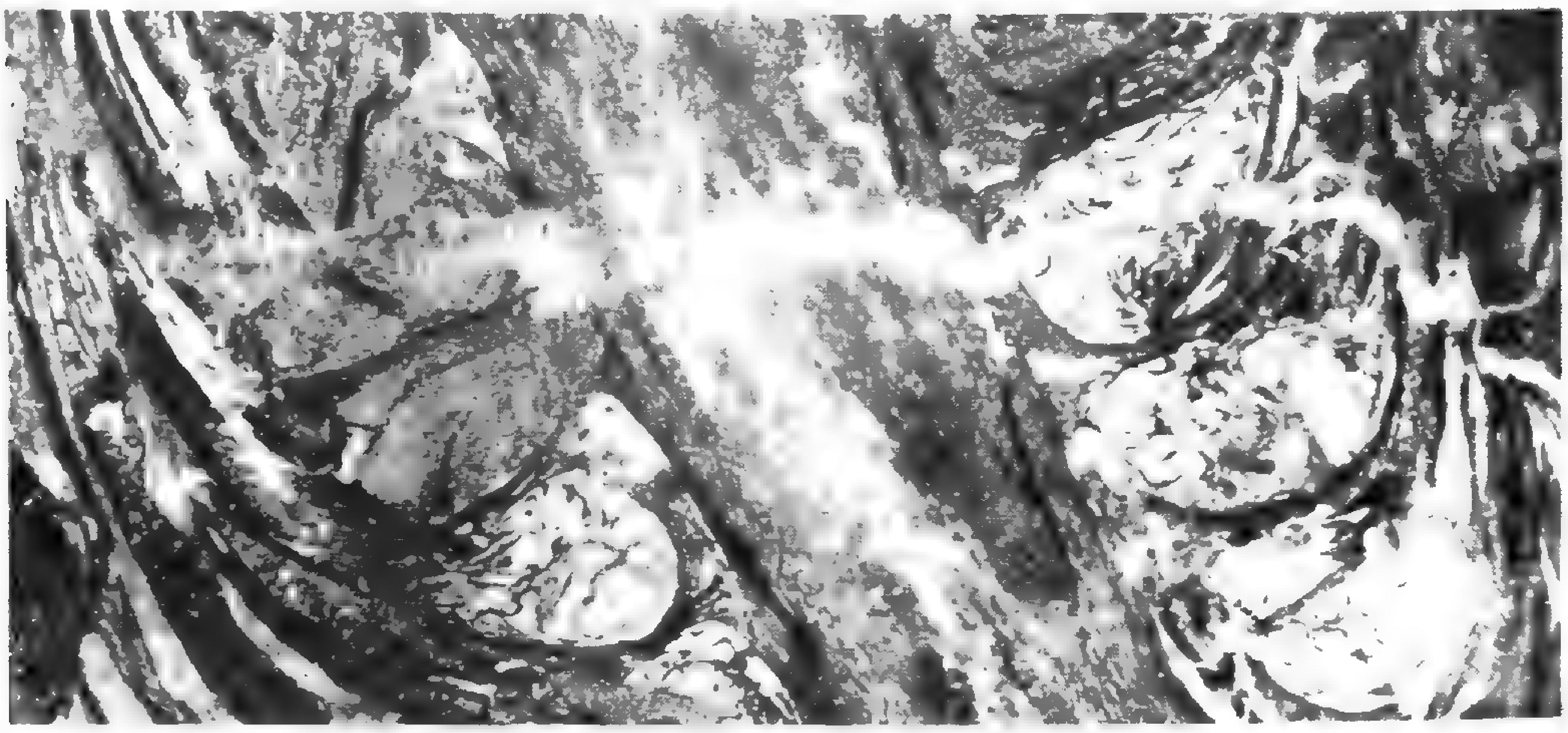

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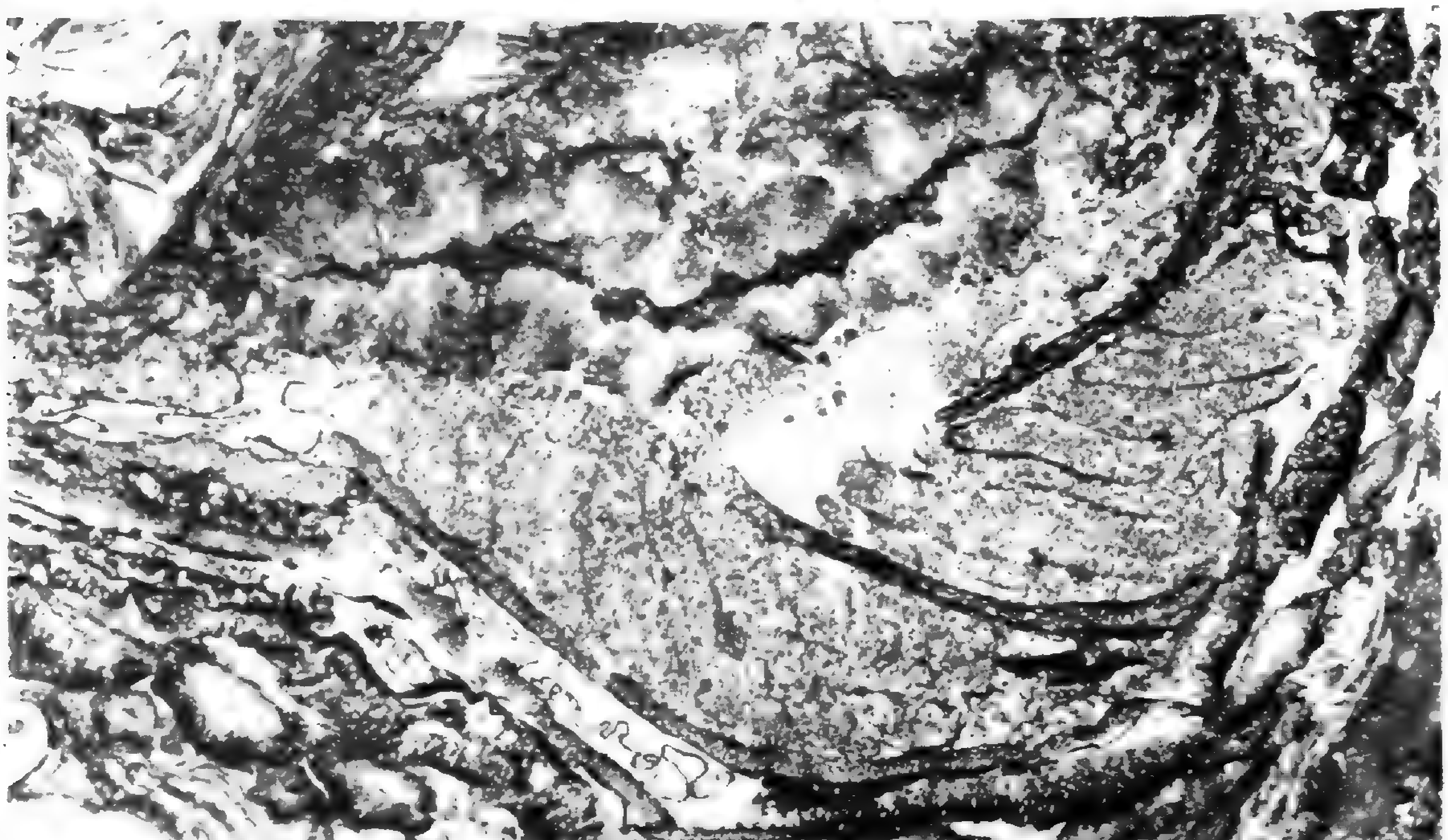


ANDERSON—AMERICAN PETRIFIED CALAMITES

EXPLANATION OF PLATE 23

Fig. 21. *Astromyelon pluriradiatum* Anderson. Cross-section of root. Coal ball no. 959. Peel 959. × 7.

Figs. 22–24. *Palaeostachya multifolia* (Reed) Anderson.

Fig. 22. Cross-section of axis at lowermost level. Coal ball no. 860. Slide 2370. × 19.

Fig. 23. Longisection of cone. Coal ball no. 860. Peel 860D-tan 20. × 4.

Fig. 24. Cross-section of cone. Coal ball no. 860. Peel 860C-b10. × 6.

EXPLANATION OF PLATE 24

Palaeostachya multifolia (Reed) Anderson

Fig. 25. External view of upper surface of bract whorl. Coal ball no. 858. × 3.

Fig. 26. Tangential section of cone showing fused bracts, sporangia, and sporangiophores. Coal ball no. 860. Peel 860C-tan 17. × 6.

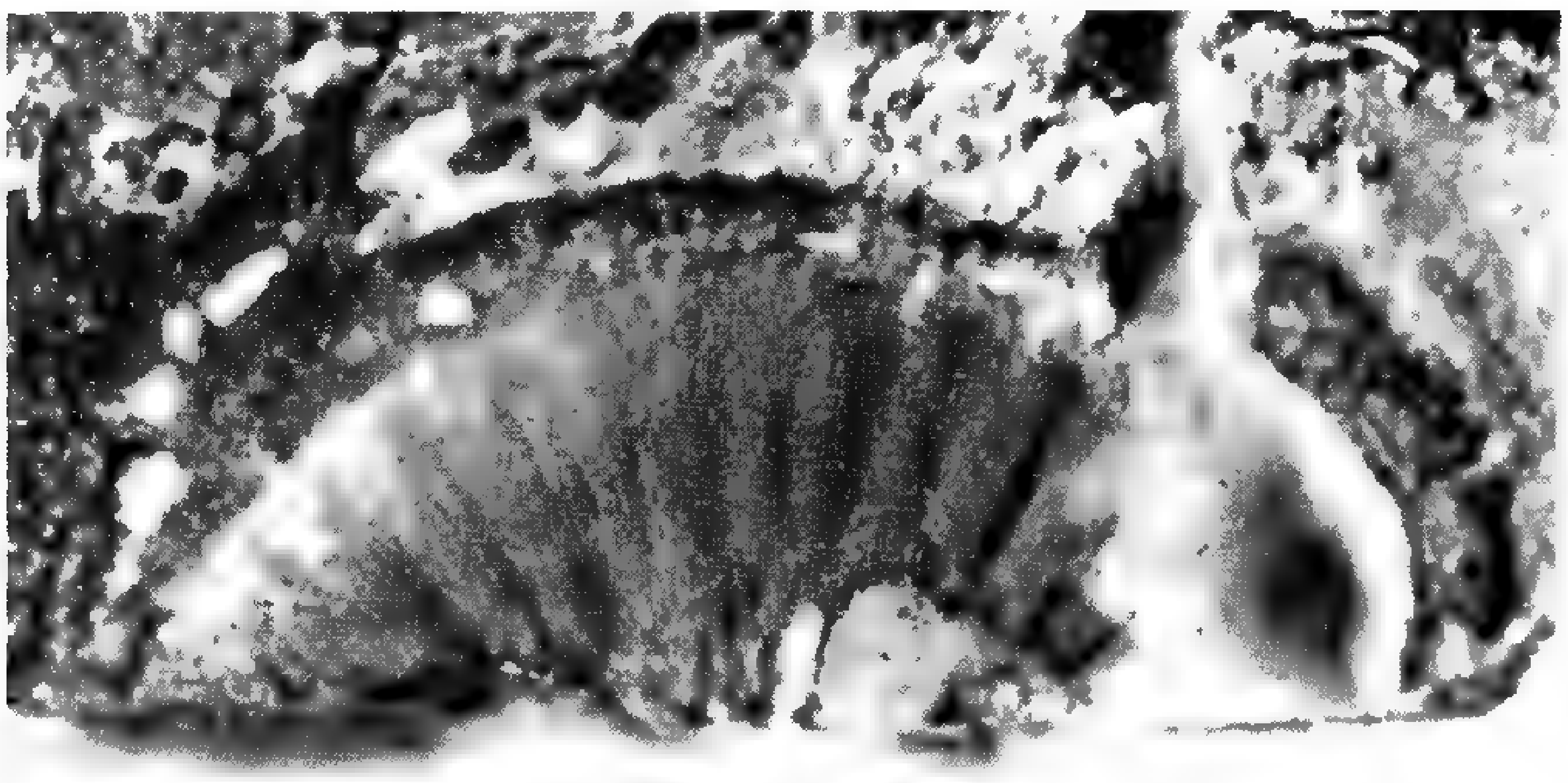
Fig. 27. Radial section of sporangia attached to upper tip of sporangiophore. Coal ball no. 839. Peel 839A2b-tan 1. × 12.

Fig. 28. Spore isolated from coal ball no. 860. Slide 2372. × 530.

Fig. 29. Scattered microspores and megaspores in sporogenous region. Coal ball no. 860. Slide 2369. × 29.

Fig. 30. Tangential section of sporangia with megaspores. Coal ball no. 858. Peel 858C1-tan 6. × 10.

Fig. 31. Cross-section of cone through developing apex. Coal ball no. 961. Peel 961A-X11. × 6.



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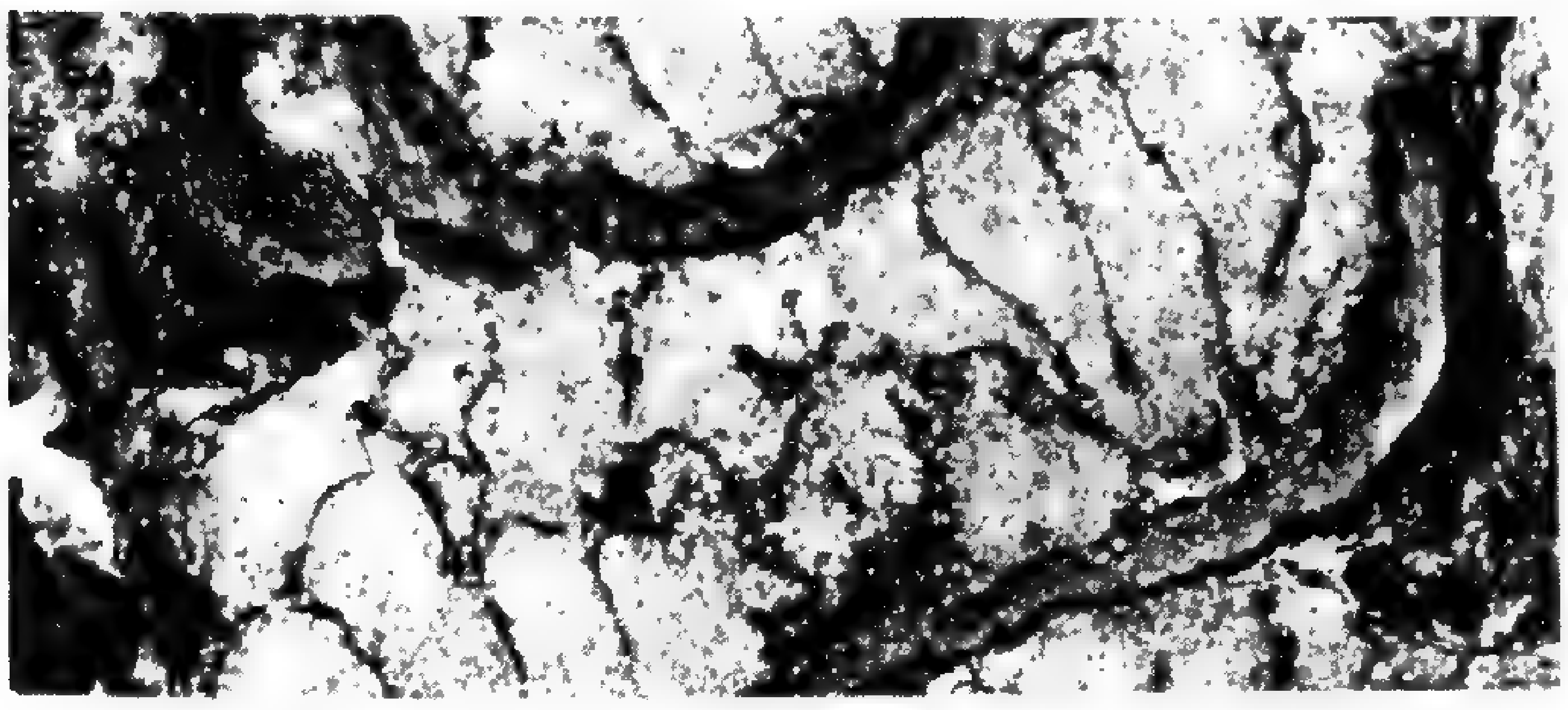

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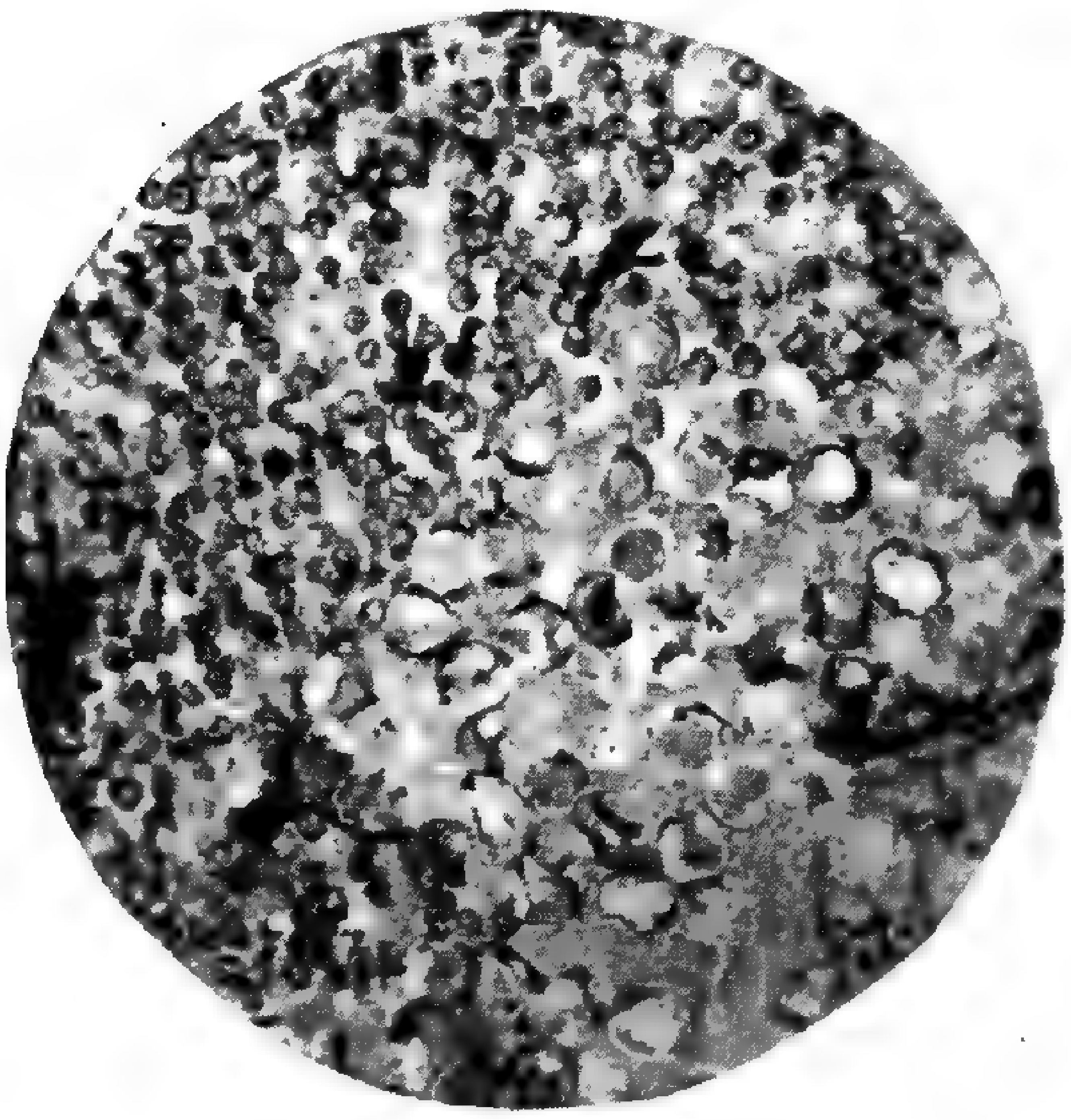

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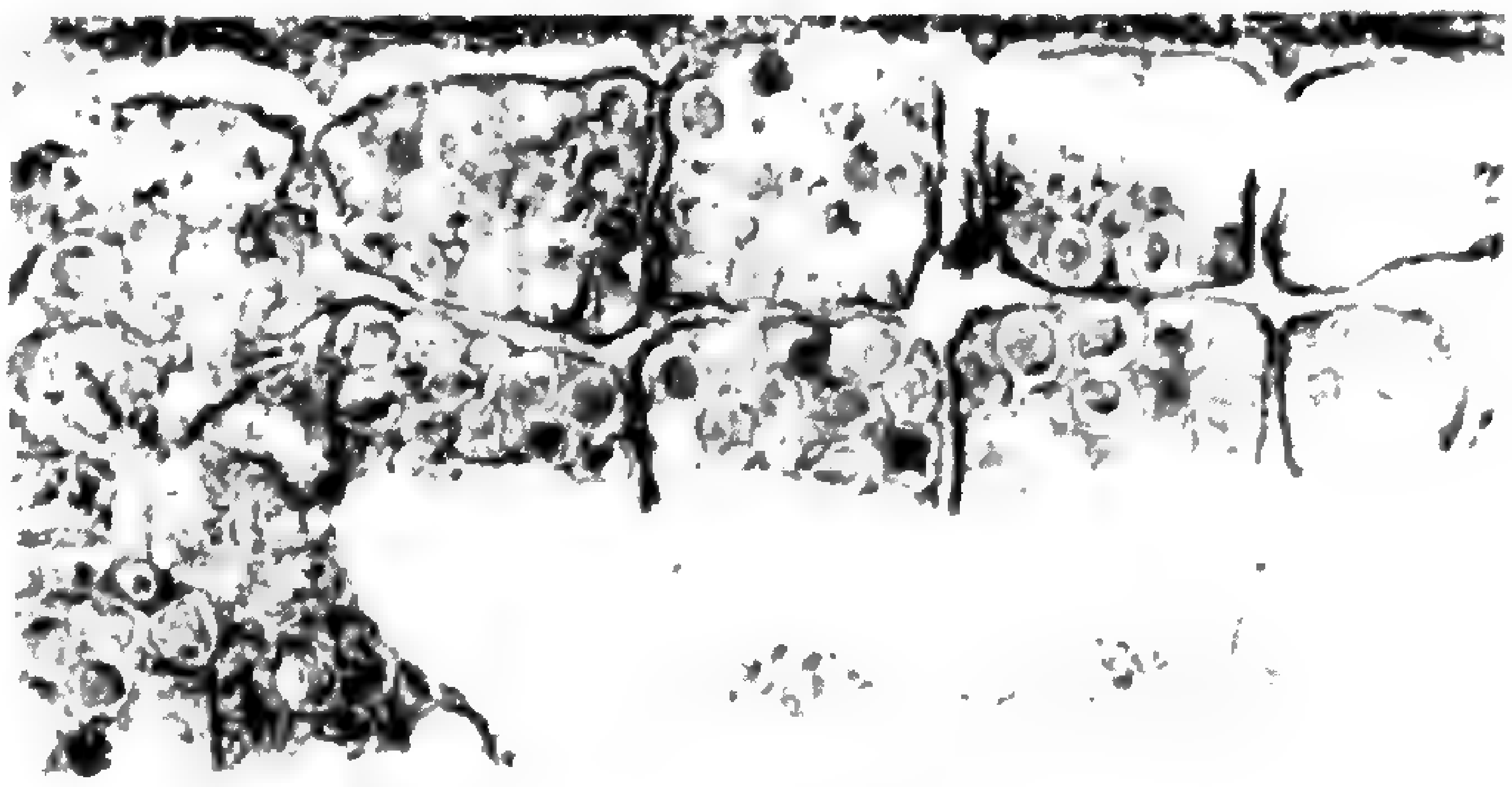

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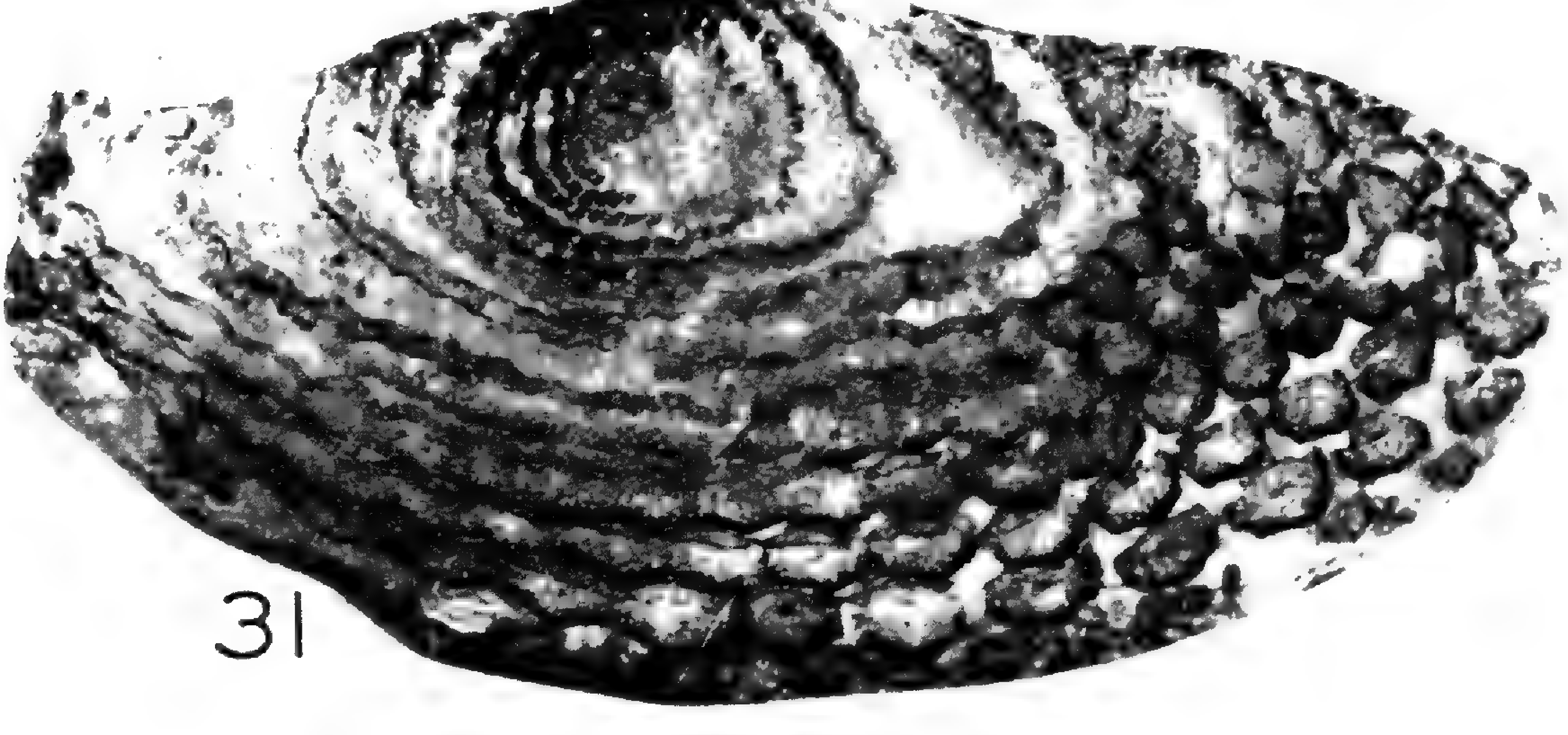

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ANDERSON—AMERICAN PETRIFIED CALAMITES

GENERAL INDEX TO VOLUME XLI

New scientific names of plants and the final members of new combinations are printed in bold face type; synonyms and page numbers having reference to figures and plates, in *italics;* and all other matter in ordinary type.